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Changing human impact on the montane forests of the eastern Andean flank, Ecuador

A thesis presented in accordance with the requirements for the degree of
Doctor of Philosophy

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MSc in Palaeobiology

BSc in Geological Sciences

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Abstract

The montane cloud forests of South America are some of the most biodiverse habitats in the world, whilst also being especially vulnerable to climate change and human disturbance. Today much of this landscape has been transformed into a mosaic of secondary forest and agricultural fields.

This thesis uses palaeoecological proxies (pollen, non-pollen palynomorphs, charcoal, organic content) to interpret ecosystem dynamics during the late Quaternary, unravelling the vegetation history of the landscape and the relationship between people and the montane cloud forest of the eastern Andean flank of Ecuador. Two new sedimentary records are examined from the montane forest adjacent to the Río Cosanga (Vinillos) and in the Quijos Valley (Huila). These sites characterise the natural dynamics of a pre-human arrival montane forest and reveal how vegetation responded during historical changes in local human populations. Non-pollen palynomorphs (NPPs) are employed in a novel approach to analyse a forest cover gradient across these sites. The analysis identifies a distinctive NPP assemblage connected to low forest cover and increased regional burning. Investigation into the late Pleistocene Vinillos sediments show volcanic activity to be the primary landscape-scale driver of ecosystem dynamics prior to human arrival, influencing montane forest populations but having little effect on vegetation composition.

Lake sediments at Huila from the last 700 years indicate the presence of pre-Hispanic peoples, managing and cultivating an open landscape. The subsequent colonization of the region by Europeans in the late 1500's decimated the indigenous population, leading to the abandonment of the region in conjunction with an expansion in forest cover ca. 1588 CE. After approximately 130 years of vegetation recovery, montane cloud forest reached a stage of structural maturity comparable to that seen in the pre-human arrival forest. The following 100 years (1718-1822 CE) of low human population and minimal human impact in the region is proposed as a shifted ecological baseline for future restoration and conservation goals. This 'cultural ecological baseline' features a landscape that retains many of the ecosystem service provided by a pristine montane forest, while retaining the cultural history of its indigenous people within the vegetation.

'... it can only be that negative results are as common in science as in other human endeavours. He who wants ancient sediments had better go where ancient sediments are, but he who seeks to answer a problem had better go where the problem is; and be prepared for the possibility of failure.'

- Paul Colinvaux, *in* Amazon Expeditions: My Quest for the Ice-Age Equator, pp-99.

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Terminology

This thesis deals with themes associated with indigenous peoples and cultures irrevocably changed by the arrival of Europeans to the Americas. The cultural and ecological impact of this event led to arguably the largest loss of distinct cultures and human life to have ever occurred. Subsequently, European colonisation has had real world impacts on the descendants of the surviving indigenous peoples. The terminology used in this thesis to characterise and identify events, acts and peoples were chosen by NJDL, who takes sole responsibility for the inaccuracies or oversimplifications of the complex and contentious issues that this thesis may touch upon. This thesis is aimed primarily at understanding the ecological and environmental change that has taken place in the montane forest of the eastern Andean flank of Ecuador through time, however, in order to address these changes, the history of the human population and their role in modifying the landscape is addressed.

Three terms used in this thesis may require clarification in order to put them into a context applicable to this work, these include:

Indigenous peoples: This term is used to refer to all peoples who lived in the Americas prior to the arrival of Europeans in 1492, and to any person after that period who would self-identify as a person of indigenous descent. In the region examined in this thesis (The Province of Napo) approximately 56.8 % still identify as of indigenous descent (2010 census) many of whom still speak regional variations of the native Quechua language.

Pre-Hispanic: The term 'pre-Hispanic' is customarily used to separate the events that occurred prior to the arrival of Europeans to the Americas, with the arrival of Christopher Columbus to The Bahamas in 1492. However, in this text the term pre-Hispanic is used in a more local context to refer to the period prior to 1532 and the arrival of Francisco Pizarro to what is now Ecuador, whose role in the collapse of the regional political power (The Incan Empire) is well documented (see Hemming, 1970; Newson, 1995; Mann, 2005).

Genocide: Genocide was defined in 1948 by the United Nations General Assembly in the 'Convention on the Prevention and Punishment of the Crime of Genocide' and is generally expressed as the systematic destruction of a culturally distinctive people, typically from the 19th century onwards. The depopulation of the American indigenous peoples after European arrival by disease, enforced starvation, reduced fertility, forced labour, migration and murder brought about by colonisation may therefore not directly meet this criteria. Contemporary first-hand written accounts by Friar Bartolomé de las Casas (1484-1566) and Bernal Díaz del Castillo (1490-1584) dispute the motivations behind the deaths associated with colonization. However, numerous works have detailed the wider events that led to the destruction of civilizations and the deaths of millions of individuals on a scale never before envisaged (Leon-Portilla, 1962; Hemming, 1970; Galeano, 1973; Mann, 2005, 2011; Levy, 2011). Here the term 'genocide' (*sensu lato*) is used to impart the colossal extent of the European driven depopulation that occurred as a result of colonization regardless of individual motivations and specific events. The events that occurred within the Quijos Valley are part of the wider 'American genocide', the depopulation of the region itself is not an act of genocide, but of European colonisation.

Table of Contents

Abstract.....	i
Acknowledgments.....	iii
Terminology.....	iv
Chapter 1	1
1 Introduction.....	1
1.1 Overview	1
1.2 Uncovering the past	1
1.3 Biodiversity hotspots.....	2
1.4 Neotropical montane forests	3
1.5 Palaeoecological methods	4
1.6 Research goal	5
1.7 Thesis structure.....	5
Chapter 2	7
2 Regional and local context of the study sites.....	7
2.1 Overview	7
2.2 Study region	7
2.2.1 Geology and physical geography.....	9
2.2.2 Climate	12
2.2.3 Vegetation.....	14
2.3 Sample locations	21
2.3.1 Huila	22
2.3.2 Vinillos.....	27
2.3.3 Modern sample 1.....	31
2.3.4 Modern sample 2.....	31

2.3.5	Modern sample 3	31
2.3.6	Modern sample 4	32
2.3.7	Modern sample 5	33
Chapter 3	34
3	Identifying environmental drivers of fungal non-pollen palynomorphs in the montane forest of the eastern Andean flank, Ecuador	34
3.1	Overview	34
3.2	Abstract	35
3.3	Introduction.....	35
3.4	The eastern Andean flank, Ecuador	38
3.4.1	Landscape	38
3.4.2	Vegetation.....	39
3.4.3	Climate	39
3.5	Study sites and samples	40
3.5.1	Huila	40
3.5.2	Vinillos.....	40
3.6	Methods	41
3.6.1	Fungal non-pollen palynomorphs.....	42
3.6.2	Environmental variables	43
3.6.3	Zonation	45
3.6.4	Data analysis	45
3.7	Results	46
3.7.1	Fungal non-pollen palynomorphs.....	46
3.7.2	Environmental variables	50
3.7.3	Canonical correspondence analysis.....	51
3.8	Discussion	52

3.8.1	Variance in fungal NPPs along a gradient of forest cover in the Andes	52
3.8.2	Fungal NPP assemblages and environmental variables	54
3.9	Conclusions.....	57
3.10	Author contributions and acknowledgments	58
Chapter 4	59
4	Landscape-scale drivers of glacial ecosystem change in the montane forests of the eastern Andean flank.....	59
4.1	Overview	59
4.2	Abstract	60
4.3	Introduction.....	60
4.4	Study site	62
4.5	Methods	64
4.5.1	Sediment sampling.....	64
4.5.2	Radiocarbon dating.....	64
4.5.3	Loss-on-ignition.....	65
4.5.4	X-ray fluorescence	65
4.5.5	Charcoal analysis.....	65
4.5.6	Palynomorph analysis	66
4.5.7	Zonation of palynomorphs	66
4.6	Results	67
4.6.1	Chronology.....	67
4.6.2	Sediments	68
4.6.3	Volcanic tephra layers.....	70
4.6.4	Macro- and micro-charcoal.....	70
4.6.5	Palynomorphs	72
4.7	Interpretation and Discussion	76

4.7.1	Depositional Environment	77
4.7.2	Glacial vegetation on the eastern Andean flank	78
4.7.3	Landscape-scale drivers of vegetation change	81
4.8	Conclusions.....	83
4.9	Author contributions and acknowledgments	84
Chapter 5	85
5	Assessing human impacts on the vegetation of the biodiverse eastern Andean flank before, and after, the arrival of Europeans (1492 CE).....	85
5.1	Overview	85
5.2	Abstract	86
5.3	Introduction.....	86
5.4	Methods	88
5.5	Chronology	89
5.6	Results	90
5.7	Discussion and conclusions	93
5.8	Author contributions and acknowledgments	96
Chapter 6	97
6	Discussion and conclusions	97
6.1	Overview	97
6.2	Introduction.....	97
6.3	Research aims.....	99
6.3.1	Research aim 1: Characterise changes in non-pollen palynomorphs across a gradient of montane forest cover	99
6.3.2	Research aim 2: Identify the environmental drivers of fungal non-pollen palynomorphs within the montane forest environment.	100
6.3.3	Research aim 3: Determine the fire regime in montane forests prior to the arrival of humans.....	102

6.3.4	Research aim 4: Assess the drivers of landscape-scale ecosystem dynamics prior to human influence on the montane forest environment.	103
6.3.5	Research aim 5: Establish the ability of pre-Hispanic indigenous peoples to impact the montane forest of the eastern Andean flank.	105
6.4	Discussion.....	106
6.4.1	Vegetation response at European arrival on the eastern Andean flank	106
6.4.2	Establishing an appropriate ecological baseline.....	110
6.5	Conclusions.....	115
6.6	Recommendations for future work.....	117
Chapter 7	121
7	References	121
Chapter 8	153
8	Appendix.....	153
8.1	Appendix A – Ecological affinity of fungal NPPs.....	153
8.2	Appendix B – Newly identified fungal NPP morphotypes.....	157
8.3	Appendix C – Chapter 5 additional figures.....	163
8.4	Appendix D – Detailed palynomorph and charcoal diagrams	165
8.5	Appendix E – Data storage	170

Figures

Figure 2.1 Map study area. (A) Map of Ecuador with Napo Province highlighted. (B) Map of Napo Province with local administrative districts or ‘Cantons’. C.J.A.T. refers to the Canton Carlos Julio Arosemena Tola. (C) Map of the Quijos Canton. Rivers are indicated in blue, black circles indicate towns and villages, and triangles represent volcanic peaks.	8
Figure 2.2 Topographical map of Ecuador. Principle Ecuadorian volcanos with Holocene activity are identified with white triangles (Hall and Mothes, 2008). Red box indicates Quijos study region.	10
Figure 2.3 The volcano Antisana (peak 5,752 m asl). Picture taken from within the montane cloud forest (ca. 2,000 m asl).....	11
Figure 2.4 Topographical map Quijos Region with active volcanos and major rivers.	12
Figure 2.5 The Neotropical ecozone containing twelve terrestrial biomes (Olson et al 2001).	15
Figure 2.6 Terrestrial ecoregions in Ecuador based on WWF (Olson et al 2001).....	16
Figure 2.7 Vegetation zones and their altitudinal extent used within this study based on those of Sierra (1999). Red line indicate modern pollen transect at Erazo (Cárdenas et al., 2014).	20
Figure 2.8 Location of samples site. Topography of the Quijos and Consanga valleys with contour lines at 500 m intervals. Red circles indicate samples sites (Huila, Vinillos and modern (M) samples), black circles indicate towns and white triangles volcanic peaks.	22
Figure 2.9 Aerial images of region around Huila. A) Quijos Valley with location of Huila in respect to the Río Quijos and the village of Cuyuja, B) Hacienda Huila and the position of Lake Huila with the pasture.	23
Figure 2.10 Huila study area. A) Lake Huila situated within its confined basin. B) Open pasture around Huila, with cloud covered montane forest present on the steeper slopes...	24
Figure 2.11 Three cross-sections through the Huila basin. Measurement where taken using a GPS, 50 m tape measure and a compass-clinometer to determine the position, size and shape of the basin. Lake depth and profile was measure using a measuring stick.....	25
Figure 2.12 Upper 1 m of the 2.09 m Huila core. The upper 1 m of the Huila core was the target of analysis. The remainder of the core consisted of the same material found below	

the tephra layer and preliminary analysis indicated that it was essentially barren of pollen (< 10,000 grains per cm ³).	26
Figure 2.13 Cross section through the Cosanga Valley from the Antisana volcano through the Vinillos section and Sumaco volcano.	27
Figure 2.14 The Vinillos section. A) Section during sampling of the sequence in 2012. B) Section one year later in 2013.	28
Figure 2.15 Vinillos profile. Sampling over two sections A (1.34 m) and B (1.84 m).	29
Figure 2.16 The Vinillos section profile with descriptions of sediment. A Munsell colour chart was used to record sediment colour. Asterisks (*) indicate location of wood macro-fossils recovered from the outcrop.	30
Figure 2.17 Location of modern sites. A) M1, B) M2, C) M3, D) M4, E) M5 (Lake Erazo).	32
Figure 3.1 Map showing position of study site and sample locations. (A) Map of Ecuador. Regions coloured black indicate an altitude of between 1300-3600 metres above sea level corresponding to Andean montane forest vegetation. (B) Map of study location with altitudinal gradient related to vegetation zones as described in the introduction and corresponding to Sierra (1999). Points indicate sample locations, squares local population centres and triangles volcanic centres.	37
Figure 3.2 Palaeoenvironmental proxies from which environmental variables have been inferred. Samples are ordered based on increasing percentage of forest pollen. Forest pollen is based on the combined percentage of <i>Alnus</i> , <i>Weinmannia</i> , <i>Hedyosmum</i> and Melastomataceae in the sample relative to the total terrestrial pollen sum. Aquatics remains relate to the percentage abundance of total aquatic remains relative to the terrestrial pollen sum. Micro-charcoal plotted as fragments per cm ³ of sediment. Organic carbon refers to the percent organic carbon loss during loss-on-ignition at 550 °C.	44
Figure 3.3 (previous pages) Fungal NPP assemblage data for all taxa occurring at > 2 % abundance in > 1 sample. Fungal NPP percentages are calculated relative to the total terrestrial pollen sum. Samples are ordered based on an increasing percentage of forest pollen.	50
Figure 3.4 Canonical correspondence analysis (CCA) of NPP morphotypes and environmental variables. NPP morphotypes (black dots) and samples (grey dots) are plotted against palaeoenvironmental proxies of environmental variables (black arrows): forest pollen (forest	

cover), aquatic remains (available moisture), micro-charcoal (regional fire regime), and organic carbon (sediment composition).....52

Figure 4.1 Study sites. **A.** Location of study site in Ecuador, within montane forest vegetation zone (1300-3600 m asl), **B.** Topographic map of study region with generalised vegetation zone from Sierra (1999). LRF-lowland rainforest; PMF – pre-montane forest; LMF-lower montane forest; MCF-montane cloud forest; UMF-upper montane forest; PAR-páramo; B/G-barren / glaciers. Black squares indicate towns, red circle is Erazo section (Cárdenas et al, 2011), and red star is the location of the Vinillos exposure. Red line represents cross-section as seen in 'D', **C.** Photograph of Vinillos exposure prior to sampling and position of Section A and B, **D.** Cross-section of eastern Andean flank through Antisana and Sumaco volcanos, with generalized vegetation zones and position of Vinillos.63

Figure 4.2 Sediment profile. Loss-on-ignition results of 48 samples indicating the percent weight loss of organic material, carbonate material and remaining inorganic material.69

Figure 4.3 TAS diagram of X-ray fluorescence data on volcanic tephra layers. T1-andesite; T2-basaltic andesite; T3-trachy-andesite; T4-dacite.70

Figure 4.4 Micro- and macro-charcoal concentrations and wood macrofossils. Micro-charcoal (< 100 µm) and macro-charcoal (> 100 µm) are displayed as fragments per cm³. Asterisk (*) mark position of individual wood macro-fossil remains.71

Figure 4.5 (*subsequent page*) Fossil pollen and spore percentage diagram from Vinillos. Taxa include types that occur at > 2 % in at least one sample. Black diamonds indicate position of radiocarbon dates (Table 4.1)72

Figure 4.6 (*previous page*) Fossil non-pollen palynomorph diagram from Vinillos based on pollen percentage. NPP morphotypes represent types that occur at > 2 % abundance of the pollen sum in at least one sample. Asterisk (*) indicates count for morphotype HdV.123 in sample at 5 cm has been divided by 10 (687% of pollen sum). Black diamonds indicate position of radiocarbon dates (Table 4.1).75

Figure 4.7 Fossil aquatic remains diagram from Vinillos based on pollen percentage. Remains include vegetative and zoological remains indicative of semi to fully aquatic conditions. Black diamonds indicate position of radiocarbon dates (Table 4.1).76

Figure 4.8 (*previous page*) Synthetic diagram of proxies used in reconstructing Vinillos section. Selected pollen taxa (*Alnus*, *Hedyosmum*, Melastomataceae, *Weinmannia*, Asteraceae and Poaceae), NPPs and charcoal are plotted as concentration per cm³. Organic

carbon is plotted as a percentage. Black diamonds indicate position of radiocarbon dates (Table 4.1).	81
Figure 5.1 Map of study region. Indigenous Quijos region located on the Eastern Andean flank of Ecuador between the Rio Coca and Rio Napo. Black circles indicate present or past population centres. Black squares are active volcanos. Red star is location of Lake Huila. ...	88
Figure 5.2 Age-depth model using Bayesian analysis. Dashed line (76-50 cm) represents a 26 cm volcanic tephra layer and is considered to have been deposited instantaneously.....	90
Figure 5.3 (<i>previous page</i>) Synthetic palaeoecological proxy diagram of Lake Huila core plotted against age. (a) Pottery shard recovered from core (42 cm), (b) Spanish arrival in Quijos region, (c) Indigenous uprising, (d) Post-colonial population and vegetation descriptions, and (e) the establishment of cattle farming in the region.....	92
Figure 5.4 DCA of (A) pollen and (B) fungal NPP data. Blue through green colour ramp correspond to palynomorph zones from Huila. Grey open circles are late-Pleistocene Vinillos samples. Grey crosses are modern surface samples (Appendix D).	93
Figure 6.1 DCA of terrestrial pollen from all samples. Arrow represents increasing human impact. A) pre-human arrival (no human impact), B) indigenous depopulation and modern environment (variable human impact), C) pre-Hispanic (intensive human impact).....	109
Figure 6.2 DCA of fungal NPPs from all samples. Arrow indicates increased disturbance by humans and volcanic activity. A) indigenous depopulation and modern environment (montane forest assemblage), B) pre-human arrival (glacial forest assemblage) and, C) pre-Hispanic (cultivated landscape assemblage).	110
Figure 6.3 DCA of pollen taxa from all sample locations indicating succession from human impacted to pristine forest (arrow). A) open landscape, B) secondary/mosaic forest, C) mature forest, and D) pristine forest.....	114
Figure 8.1 New fungal morphotypes described from the eastern Andean flank of Ecuador. Conidia positioned with proximal cell at bottom. 1, OU-5; 2, OU-18; 3, OU-28 a-c; 4, OU-35; 5, OU-100; 6, OU-101; 7, OU-102; 8, OU-103; 9, OU-104; 10, OU-105; 11, OU-106; 12, OU-107; 13, OU-108; 14, OU-109; 15, OU-110; 16, OU-111; 17, OU-112; 18, OU-113; 19, OU-114; 20, OU-115; 21, OU-116; 22, OU-117; 23, OU-118; 24, OU-119; 25, OU-120.....	161
Figure 8.2 The Quijos Valley. Vegetation zones are based on those of Sierra (1999). Black circles indicate population centres. The indigenous village of Hatunquijos no longer exists,	

the position is recorded in Newson (1995). Red circles indicate the location of samples taken.	163
Figure 8.3 TAS diagram. Geochemical data from X-Ray florescence (XRF) analysis plotted onto a total alkali-verses-silica (TAS) diagram characterises the Lake Huila volcanic tephra layer as a dacite.	164
Figure 8.4 Modern pollen and fungal NPP diagrams. Samples plotted on an increasing altitudinal gradient.	165
Figure 8.5 (Page 164-165) Huila pollen diagram. Pollen count incorporates terrestrial taxa excluding Poaceae. Pollen percentage diagram of taxa that occur at > 2% and <i>Zea mays</i> . .	167
Figure 8.6 Huila fungal NPP diagram. Plotted as a percentage of the total non-Poaceae pollen sum.....	168
Figure 8.7 Macro- Micro-charcoal and organic content diagram of Huila.....	169

Tables

Table 2.1 Vegetation zones and their altitudinal extent used within this study based on those of Sierra (1999) (<i>left</i>).....	17
Table 2.2 Summary of the samples collected in the field and the number subsampled for analysis. Details of sample locations and characteristics can be found within the Appendix (Table 8.1).	33
Table 3.1 Radiocarbon (AMS) ages obtained from palynomorph residues from Huila and Vinillos. The dated sample from Huila is from the base of the sediment analysed, i.e. all the samples presented here are younger than the age of this sample. The dated sample from Vinillos is from the upper part of the sedimentary section, i.e. all the samples presented here are older than the age indicated. Original dates calibrated in OxCal 4.2.4 (Bronk Ramsey et al., 2013) using IntCal13 atmospheric curve (Reimer et al., 2013).....	41
Table 3.2 Abbreviations of taxa used in NPP diagram (Fig. 3.3) and CCA diagram (Fig. 3.4)..	47
Table 4.1 Accelerator mass spectrometry (AMS) radiocarbon (¹⁴ C) dating of Vinillos palynomorph residues.	67
Table 5.1 Accelerator mass spectrometry (AMS) radiocarbon (¹⁴ C) dates of Huila palynomorph residues.	89
Table 8.1 Details and locations of samples taken.	163
Table 8.2 Geochemistry of standards and the Huila tephra layer using XRF. *Loss on ignition (LOI) was undertaken at 550°C for 2 hours.	164
Table 8.3 Modern population within the region identified as the Quijos Chiefdom / Gobernación de Los Quijos. *Information from Ecuadorian census http://www.ecuadorencifras.gob.ec/censo-de-poblacion-y-vivienda/	164

Chapter 1

1 Introduction

1.1 Overview

Chapter 1 introduces the rationale behind the research presented in this thesis. The overarching research goal of understanding how the tropical montane cloud forest of the eastern Andean flank of Ecuador has responded through time to changes in human impact is discussed and the aims to achieve this goal are identified.

1.2 Uncovering the past

The study of past environmental and ecosystem change can offer insights into how the world may respond to continuing human impact. To understand the past a fundamental principle is required, that being uniformitarianism. The concept of uniformitarianism was conceived by James Hutton (1795) and was subsequently honed by his contemporaries John Playfair (1802) and Charles Lyell (1830). The precise definition of uniformitarianism has been refined over time (Scott, 1963; Gould, 1965), but essentially utilizes the philosophical

principle of ‘actualism’ to establish the *a priori* assumption that the same natural laws and processes occur through time and space. Charles Lyell’s books on the ‘Principles of Geology’ incorporated the axiom “*the present is the key to the past*” to encapsulate this concept into our understanding of the Earth’s physical processes. Palaeoecology utilises the principle of uniformitarianism, applying it to the Earth’s biological processes. The application of this approach to the ecology of the past is the foundation of palaeoecology, which can be stated as “*the branch of ecology that studies (the) past (of) ecological systems and their trends in time using fossils and other proxies*” (Rull, 2010). Reconstructing past environments and ecosystems allows for their response to drivers of change, such as long-term climate trends or human impact, to be assessed on time scales longer than that of real-time experiments or observations. This temporal aspect of palaeoecology and its multiproxy nature allows us to offer predictions of future ecosystem dynamics in settings that have no modern analogue, allowing us to expand on Charles Lyell’s axiom to advocate that the past is the key to the future.

1.3 Biodiversity hotspots

Patterns in global biodiversity have been deliberated upon at least as far back as the early 19th century, when preeminent naturalists such as Alexander von Humboldt and Alfred Russell Wallace observed the abundant richness of species near the equator (Humboldt, 1850; Wallace, 1878). Increased species diversity has also been identified in mid-elevation settings across altitudinal gradients, a concept perhaps linked to equatorial diversity (MacArthur, 1969; Terborgh, 1977). However, despite a plethora of climatic, ecological and evolutionary hypotheses proposed, a definitive consensus as to the causal factors behind this ‘mid-domain’ increase in species richness is still absent (Rohde, 1992, 1997; Rosenzweig, 1992; Rosenzweig & Sandlin, 1997). One hypothesis is that the increased species diversity in mid-domain settings is in fact an emergent property of the geometry of a constrained setting, in that “*the increasing overlap of species ranges towards the centre of a shared geographic domain [is] due to geometric boundary constraints in relation to the distribution of species’ range sizes and midpoints*” (Colwell & Lees, 2000). This ongoing area of research in biogeography has led to the same conclusion, that equatorial, mid-elevation environments are some of the most biodiverse habitats on the planet, and are therefore the

perfect environments in which to attempt to understand the mechanics behind key ecological processes through time. The palaeoecology of the Neotropics is still a somewhat new area of research in comparison to that of the northern temperate region. A number of long records have begun to disentangle the ecosystem dynamics driven by changes in climate across the continent (Hooghiemstra, 1984; Baker et al., 2001; van der Hammen & Hooghiemstra, 2003; Bush et al., 2004b; Bogotá-A et al., 2011; Hanselman et al., 2011). However, further work is essential in order to provide a comprehensive insight into the response of Neotropical vegetation to drivers of ecosystems change.

1.4 Neotropical montane forests

The Republic of Ecuador, located in equatorial South America, is one of the most biodiverse countries in the world. However, a high degree of species endemism in conjunction with rapid habitat destruction means that it is also one of the most at risk of ecosystem degradation (Henderson et al., 1991; Heywood, 1995; Myers et al., 2000; Brooks et al., 2006; FAO, 2006; IPCC, 2013). Ecuador can be split into three ecological zones, each part of a wider biodiversity hotspot in its own right; 1) coastal Ecuador and Colombia, 2) the tropical Andes, and 3) western Amazonia (Myers et al., 2000; Brooks et al., 2006). The immense diversity of Amazonian species was previously thought to have been driven by Pleistocene aridity, forming forest fragments ('refugia') isolated within a vast savanna (Haffer, 1969). However, palaeoecological records have shown the Amazon to have been forested throughout much of last glacial period, with vegetation responding to heterogeneous changes in climate across the continent, but no wholesale replacement of tropical lowland rainforests (Liu & Colinvaux, 1985; Bush et al., 1990, 2004a; Haberle, 1997; Colinvaux et al., 2000). The origin of Amazonian biodiversity has been pushed back in time by fossil and phylogenetic evidence (Jaramillo et al., 2006; Rull, 2008), although the exact mechanisms that drove diversification remain unclear (Bush, 1994; Hoorn et al., 2010). The montane forests of the eastern Andean flank emerge at the convergence of the tropical Andes and western Amazonia, forming a distinctive narrow band of tropical montane forest vegetation, located in a heterogeneous and dynamic landscape. Half of the plant species in Ecuador occur within montane forests, which covers less than 10 % of the country's landmass (Webster, 1995). Estimates of human impact on Ecuadorian montane forests

suggests < 7 % of the forest remains intact, with ca. 4 % remaining on the western Andean flank, and almost nothing within the central Andean valley (Dodson & Gentry, 1991). The montane forest of the eastern Andean flank, at the edge of the Amazon basin is thought to contain more intact forest due to its large areas of protected forest, its relatively late human occupation, and the difficulty in cultivate crops on its steep and largely inaccessible slopes (Gentry, 1995; Webster, 1995). However, whether any Neotropical forests are indeed completely intact, or the remnants of vegetation recovery after disturbance by pre-Hispanic indigenous peoples is open to debate (Heckenberger et al., 2003; Barlow et al., 2012; McMichael et al., 2012b, 2017; Clement et al., 2015; Levis et al., 2017).

1.5 Palaeoecological methods

In this thesis a multiproxy palaeoecological analysis, incorporating independent yet complimentary proxies, is used to reconstruct the ecological history and changing human impact of a mid-elevation equatorial forest. Analysis of plant pollen and spores is used as a proxy of vegetation composition and structure, providing an understanding of past vegetation dynamics (von Post, 1929). Charcoal is used to interpret the fire regime, using macro-charcoal (> 100 μm) to identify local fires and micro-charcoal (< 100 μm) to establish regional fire conditions (Whitlock & Larsen, 2001). Non-pollen palynomorphs (NPPs) are incorporated into this study as an independent proxy of a variety of ecosystem process (van Geel, 2001). NPPs are an exceptionally useful, if underused proxy capable of providing information on a variety of ecosystem processes from vegetation change and erosional processes, to human and animal impact and aquatic properties (van Geel & van der Hammen, 1978; Pals et al., 1980; van Geel et al., 2003; Davis & Shafer, 2006; Gill et al., 2013). Sediment physical characteristics are also assessed, with carbon content (Loss-on-ignition) and chemical properties (X-ray fluorescence) analysed to provide information on the depositional environment and the dynamic physical processes underway on the eastern Andean flank of Ecuador. The methods used to sample, prepare, count and analyse these proxies are individually described within the chapters they are used (Chapter 3, 4 & 5).

1.6 Research goal

The overarching goal of this research is to understand how the biodiverse tropical montane forest of the eastern Andean flank of Ecuador has responded through time to changes in human impact. Vegetation is investigated during four distinct phases, characterised as: 1) pre-Human arrival (control), 2) pre-Hispanic indigenous occupation, 3) European colonization, and 4) post-independence modern habitation. In order to realise this overarching research goal five objectives are targeted.

- 1) Characterise changes in non-pollen palynomorphs across a gradient of Neotropical montane forest cover.
- 2) Identify the environmental drivers of fungal non-pollen palynomorphs within the montane forest of the eastern Andean flank.
- 3) Determine the fire regime in a Neotropical montane forests prior to the arrival of humans.
- 4) Assess the drivers of landscape-scale ecosystem dynamics in a montane a forest environment prior to the arrival of humans.
- 5) Establish the ability of pre-Hispanic indigenous peoples to impact the montane forest of the eastern Andean flank.

1.7 Thesis structure

Chapters 3-5 present the main scientific achievements of this study and have been published in (Chapter 3 and 4) or are in review (Chapter 5) international journals. Chapter 3 addresses aims 1 and 2, Chapter 4 addresses aims 3 and 4, and Chapter 5 addresses aim 5. Overall, these chapters aim to contribute to our understanding of ecosystem dynamics and past human impact on the montane forests of the eastern Andean flank. The chapters of this thesis are:

Chapter 1 (*This chapter*) – An introduction to the background and themes that this work investigates and a statement of the aims and overarching research goal.

Chapter 2 – An overview of the climate, vegetation and geology of the study regions and specific details of the study sites.

Chapter 3 – A methodological chapter utilizing a novel approach to non-pollen palynomorph analysis to better understanding the response of montane forests to ecosystem drivers.

Chapter 4 – A palaeoecological reconstruction of a pre-human arrival montane forest, using a multiproxy analysis to detail the landscape-scale drivers at work in montane environments.

Chapter 5 – A multiproxy analysis describing the response of montane forests to changing human impact through time, and incorporating the previous two chapters into a discussion of vegetation recovery during human depopulation.

Chapter 6 – Reviews and discusses the research aims examined within Chapters 3-5. A discussion of the overriding research question and its wider implications are elaborated upon and conclusions reached.

Chapter 2

2 Regional and local context of the study sites

2.1 Overview

In this chapter the characteristics of the study region and the specific study sites are described. The climate, vegetation, geology and physical geography of the region are discussed in order to put the drivers of ecosystem change into context. Each individual study site is also reviewed, detailing their specific settings and the methodology involved in recovering samples.

2.2 Study region

The samples analysed in this study are from the Quijos Canton in the Napo Province of northern Ecuador (Fig. 2.1). The Quijos Canton covers a region of ca. 1577 km² on the eastern Andean flank, approximately 40 km south-east of the capital city Quito.

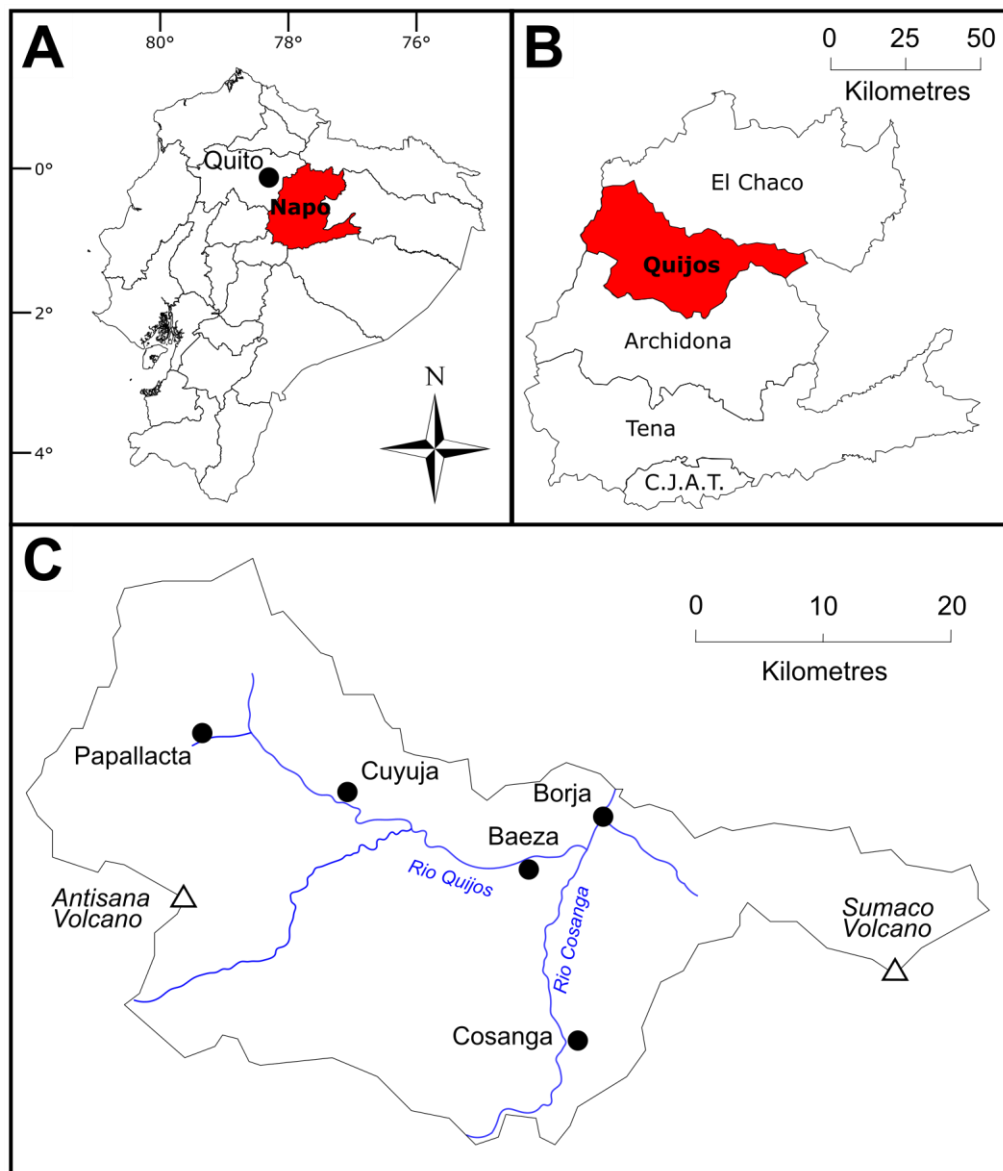


Figure 2.1 Map study area. (A) Map of Ecuador with capital city (Quito) and Napo Province highlighted. (B) Map of Napo Province with local administrative districts or ‘Cantons’. C.J.A.T. refers to the Canton Carlos Julio Arosemena Tola. (C) Map of the Quijos Canton. Rivers are indicated in blue, black circles indicate towns and villages, and triangles represent volcanic peaks.

2.2.1 Geology and physical geography

2.2.1.1 Ecuadorian Andes

The physical geography of South America is dominated by the Andean mountain chain which extends 9000 km along its western coast. Uplift of the northern Andes began around 25 million years ago at the end of the Paleogene and was driven by the subduction of the Nazca Plate beneath the South American Plate (Montgomery et al., 2001). The basement rocks were formed during in the Palaeozoic, metamorphosed throughout the Cretaceous, and later overlain by sedimentary deposits during the Neogene and Quaternary (Feininger, 1982; Neill, 1999a; Vera, 2013). Persistent volcanic activity throughout the Neogene and Quaternary increased the height of the Andes, with numerous volcanic peaks along the western and eastern flanks of Ecuador exceeding 5000 m asl (e.g. Antisana, Cotopaxi, Chimborazo, Tungurahua) (Vera, 2013). Volcanic eruptions throughout the Quaternary have deposited thick layers of volcanic ash (tephra layers) throughout Ecuador, with at least 20 volcanos active during the Holocene (Fig. 2.2) (Hall & Mothes, 2008; Hall et al., 2008). The eastern Andean flank of northern Ecuador forms a steep slope rising 5000 metres in altitude from the Amazonian lowlands (< 700 m asl) to the volcanic peak of Antisana (5752 m asl) in around 50 km. This abrupt change in topography leads to gaps in vegetation and areas of early successional forest where rapid erosion and landslide events have occurred, particularly during periods of increased precipitation (Stern, 1995; Bussmann et al., 2008). High fluvial activity in the wet tropical Andes transports eroded sediments downstream towards the Amazon, contributing to landscape heterogeneity and the formation of steep sided valleys perpendicular to the eastern Andean flank.

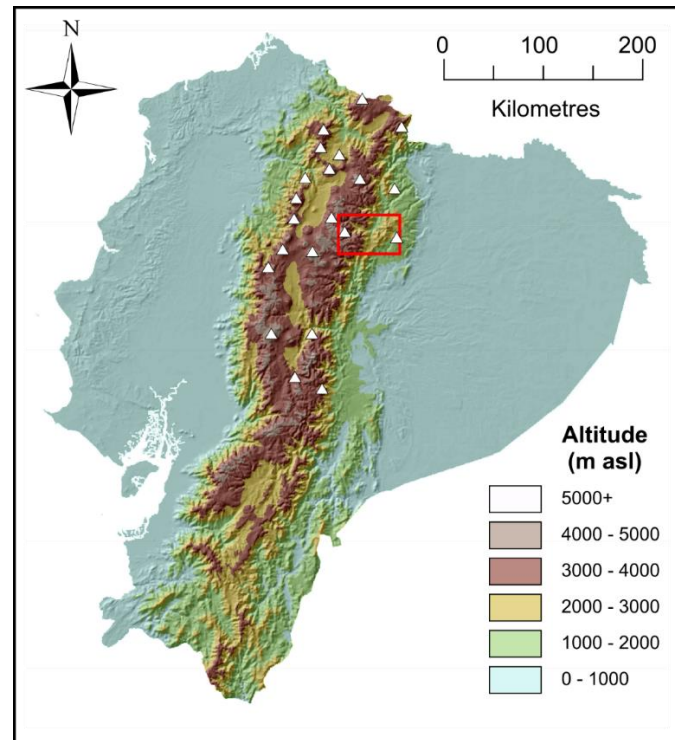


Figure 2.2 Topographical map of Ecuador. Principle Ecuadorian volcanos with Holocene activity are identified with white triangles (Hall and Mothes, 2008). Red box indicates Quijos study region.

2.2.1.2 The Quijos Region

The Quijos Canton contains a varied topography, rising from an altitude ca. 1200 m asl near the base of the Sumaco volcano to 5752 m asl at the peak of the Antisana volcano (Fig. 2.3). The underlying geology of the region is the same as that described in the previous section (2.2.1.1) for the Ecuadorian Andes. Quaternary sediments overlay a metamorphic basement consisting of a 'pelitic mica schist and phyllite, with minor chlorite-rich metavolcanic rocks, quartzite and marble (Feininger, 1982). Fluvial activity is a vital physical driver of landscape dynamics in the region with the Río Quijos flowing from the high altitude Páramo grasslands around Papallacta and Antisana and the Río Cosanga from the montane forest slopes of the Cosanga Valley (Fig. 2.4). Water from the Río Quijos, Río Cosanga and their numerous smaller tributaries eventually flows north joining the Río Coca and eventually the Amazon River. The active volcanos Antisana and Sumaco located to the west and east of the study region respectively have a major importance to the geomorphology and sediment composition of the region.



Figure 2.3 The volcano Antisana (peak 5,752 m asl). Picture taken from within the montane cloud forest (ca. 2,000 m asl).

Antisana is an andesitic stratovolcano built in three phases, whose eruptive and geological history was poorly known until recently, and whose older edifices have undergone explosive eruptions and remodelling by glacial erosion (Bourdon et al., 2002; Hall et al., 2017).

Antisana's most recent edifice has seen > 50 eruptions of andesitic and dacitic lavas and tephra occur throughout the late Pleistocene and Holocene (Hall et al., 2017). Tephra chronology indicates the most recent eruption occurred at least 800 years ago, however, smoke was observed coming from its edifice in 1802 by the explorer and naturalist Alexander von Humboldt (Hall et al., 2017).

Sumaco is a small stratovolcano situated to the east of Antisana, separated from the main Andean mountain chain in a back-arc setting (Hall et al., 2008). Sumaco is unique in the northern Andes being the only major volcanic source of basaltic lavas, and therefore chemically distinct from the andesitic lavas characteristic of the Andes (Bryant et al., 2006). Sumaco's steep-sided symmetrical cone has been used to infer its relative youthfulness in comparison to the rest of the Andes, however, a paucity of work in this region means its history is poorly understood and only ambiguous reports of an eruption in 1895 indicate it is still extant (Global Volcanism Program, 2017).

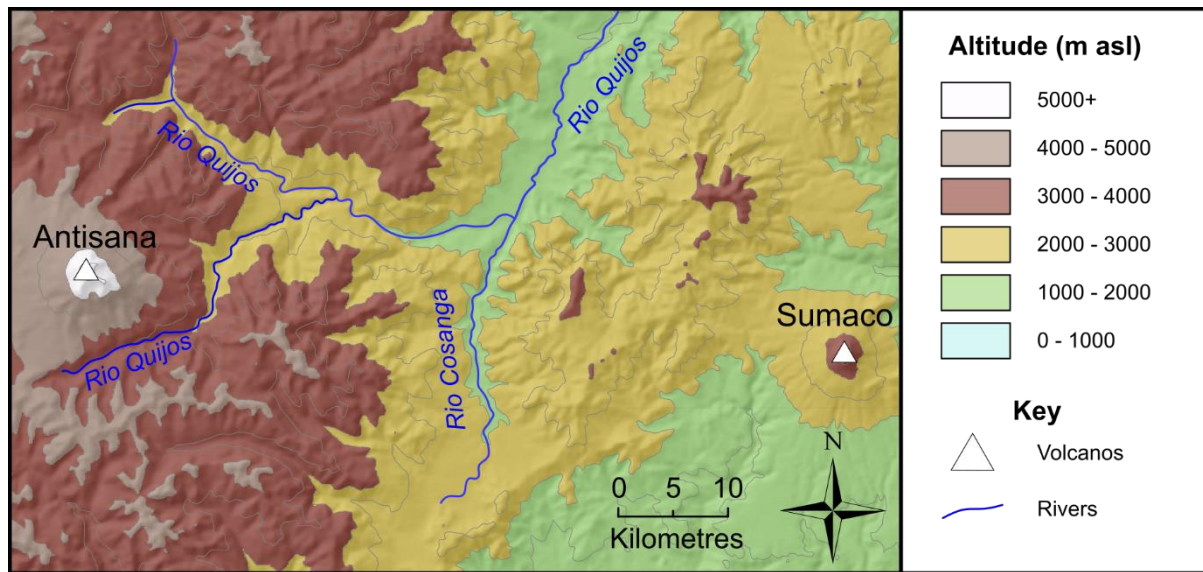


Figure 2.4 Topographical map Quijos Region with active volcanos and major rivers.

2.2.2 Climate

2.2.2.1 Tropical South America

The climate of tropical South America is driven by the migration of the Intertropical Convergence Zone (ITCZ) over the Pacific and Atlantic oceans, and seasonal variation in the South American Summer Monsoon (SASM) over the continental interior (Garreaud et al., 2009; Flantua et al., 2016). The ITCZ, sees warm easterlies converge over tropical South America, leading to increased rainfall north of the equator during the austral winter (June to August). Migration of the ITCZ south during the austral summer (December to February) leads to heavy precipitation within the Amazon and eastern Andes in association with the development of a monsoon system (SASM) (Garreaud et al., 2009; Bush & Gosling, 2012). Interaction of these atmospheric systems with ocean currents, continental topography, vegetation and soil moisture modify the climate over tropical South America, leading to variable levels of precipitation.

2.2.2.2 *The eastern Andean flank*

Atmospheric circulation and climate in tropical South America is highly influenced by the Andes which rises to 6268 m asl in Ecuador. The decrease in temperature with increased elevation over complex Andean terrain is estimated to occur at $\sim 6.9^{\circ}\text{C}$ per 1000 m (Córdova et al., 2016). High precipitation on the eastern Andean flank is driven by orographic rainfall as moist air that has travelled across the Amazon is driven upwards and cooled (Garreaud et al., 2009).

2.2.2.3 *The Quijos region*

Temperature within the Quijos region is primarily a function of altitude which ranges from 5704 m asl at the peak of the Antisana volcano to ca. 1200 m asl at the base of the Sumaco volcano. The position of the Quijos region near the equator means that seasonal changes to solar radiation are minimal and that an adiabatic lapse rate can be used to estimate temperatures between the study locations, which range in altitude from 1798-2611 m asl, and by incorporating the limited temperature data available for the region.

Mean annual daytime temperatures for the town of Baeza (1915 m asl) are frequently recorded within the range of 16-20 °C (Cordovez, 1961; Harling, 1979; Valencia, 1995; Galeas & Guevara, 2012). However, data from Grubb and Whitmore (1966) record mean monthly daytime temperatures at Baeza throughout 1931 with a minima of 12-15°C and maxima of 21-26°C, suggesting a wider range of daytime temperatures may be occurring. Unpublished data from Unger et al. (2010) record a mean annual temperature of only 14.3°C near the base of the Sumaco volcano at a similar altitude as Baeza (1915 m asl). This may suggest that temperature change by elevation is too simplistic a measure and that the physical geography and variable cloud cover cannot be excluded in estimating temperature change along altitudinal gradient within the Quijos Valley.

Precipitation in the Quijos region is driven predominantly by warm moist air from the southern Atlantic, condensing as it ascends through the Andes, and precipitating out as orographic rainfall. High levels of evapotranspiration across the Amazon allows for active upslope cloud convection, meaning that the eastern Andes slopes are almost continuously wet (Neill & Jørgensen, 1999). Historical measurements of precipitation in Baeza have been

recorded as 2165 mm (Grubb and Whitmore 1966), 2320mm (Valencia, 1995), 2200 mm (Cordovez, 1961) and 2456 mm (Cuéllar, 2009) per annum, with similar measurements near Cuyuja with an average of 2141mm of rainfall per annum between 1950-1961 (Grubb & Whitmore, 1966). However, annual rainfall figures likely underestimate total precipitation, as ground level cloud contact is poorly measured in traditional rain gauges (Grubb & Whitmore, 1966). The stripping of moisture from ground level cloud by vegetation is particularly important during the ‘less wet’ months (November-February in the Quijos region) when it may exceed that provided by vertical rainfall (Still et al., 1999).

2.2.3 Vegetation

2.2.3.1 Neotropical vegetation

The Neotropics contain twelve biomes which are characterised by their broad plant and animal communities, having formed in response to specific physical and climatic conditions (Fig. 2.6) (Olson et al., 2001). Tropical South America is dominated by the ‘tropical and subtropical moist broadleaf forest’ biome, which is distinguished by its low seasonality, high levels of precipitation and lowland evergreen rainforest (Olson et al., 2001). ‘Montane grasslands and shrublands’ of the high Andes and ‘tropical and subtropical grasslands, savannas and shrublands’ of the Llanos (north) and Cerrado (south) surround the ‘tropical and subtropical moist broadleaf forest’ biome of the Amazon Basin (Fig. 2.5), making this region a centre of global biodiversity and a conservation priority (Myers et al., 2000; Malhi et al., 2008).

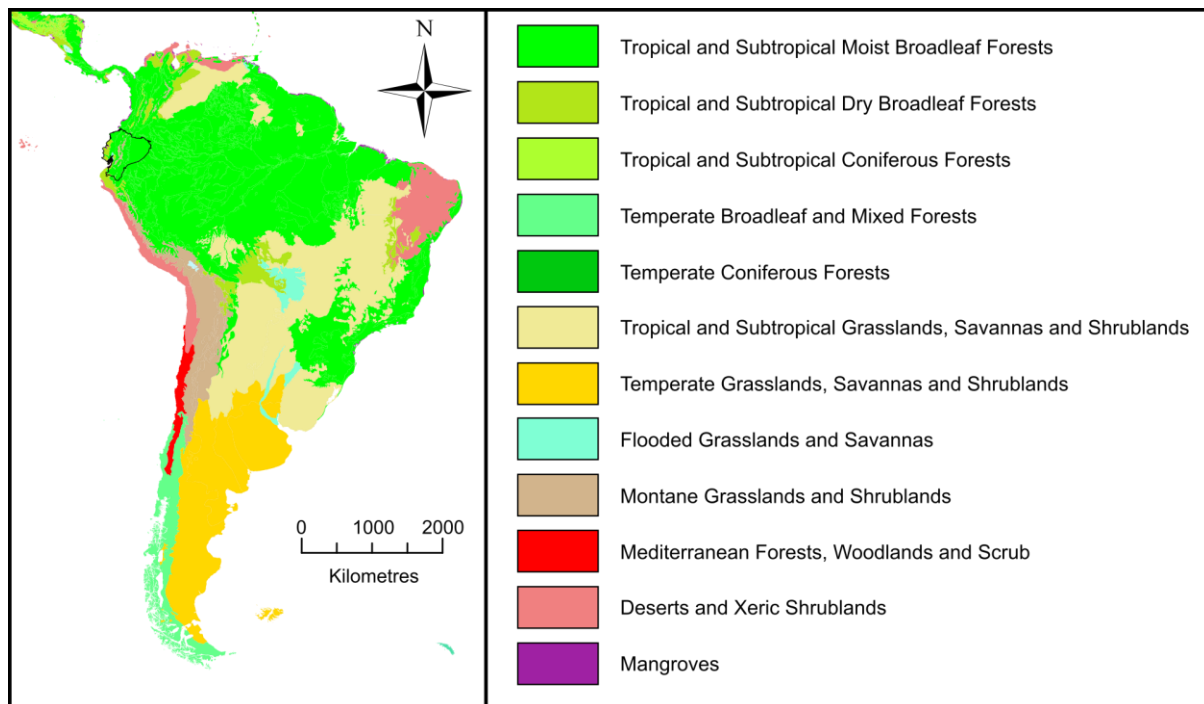


Figure 2.5 The Neotropical ecozone containing twelve terrestrial biomes (Olson et al 2001).

2.2.3.2 Ecuadorian vegetation

Ecoregions are subdivisions of the larger biomes and consist of a geographic area with a distinct assemblage of natural communities, and a commonality of species and environmental conditions (Olson et al., 2001). Ecuador contains twelve (12) terrestrial ecoregions ranging from coastal mangroves, to high altitude páramo and lowland rainforests, here I focus on the ‘eastern cordillera real montane forest’ (Fig. 2.6). The ‘eastern cordillera real montane forest’ ecoregion extends along the eastern Andean flank of northern Peru, Ecuador, and southern Colombia covering an area of approximately 10 million hectares and separating the grasslands of the ‘northern Andean páramo’ from the western Amazonian ‘Napó moist forest’ (Fig. 2.6). This distinctive tropical montane forest environment is located within the ‘tropical Andean biodiversity hotspot’, which contains over 20,000 endemic plant species, comprising 6.7 % of all plant species world-wide, making it a ‘hyper-hot’ candidate for conservation (Myers et al., 2000).

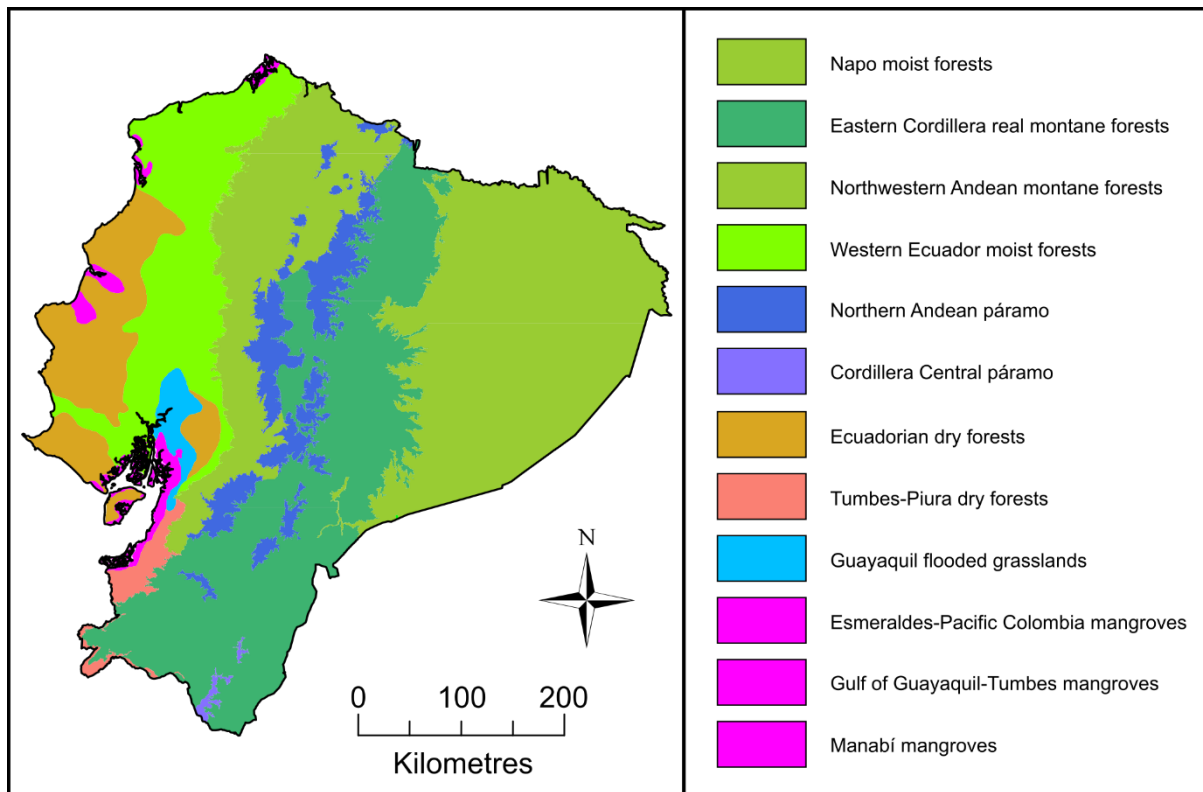


Figure 2.6 Terrestrial ecoregions in Ecuador based on WWF (Olson et al 2001).

2.2.3.3 Eastern Andean flank vegetation

Numerous hierarchical systems for dividing and classifying vegetation across the steep Ecuadorian Andes have been published (Grubb, 1971; Acosta Solís, 1977; Harling, 1979; Cañadas, 1983; Gentry, 1995; Neill, 1999b; Valencia et al., 1999). Here I use a translation of the Spanish classification system developed by Sierra (1999), which unlike the former systems incorporates regional variation in floristic composition. The region studied within this work lies within the phytogeographical range of the northern region of the eastern Andean flank (Table 2.2), which correspond to the northern portion of the 'eastern cordillera real montane forest' ecoregion. The montane forests within the area of interest are divided into three characteristic montane forest vegetation zones, preceded by a pre-montane transition zone. The, i) lower montane forest, ii) cloud forest, and iii) upper montane forest occur between 1300-3400 m asl above which vegetation transitions into a high elevation páramo (grassland) (Table 2.1).

Table 2.1 Vegetation zones and their altitudinal extent used within this study based on those of Sierra (1999) (*left*).

<i>Región Andina</i>		<i>Andean Region</i>
<i>Estribaciones Orientales</i>		<i>Eastern Flank</i>
<i>Norte</i>	<i>Altitud / Altitude</i>	<i>Northern</i>
Piemontano	600-1,300 m asl	Pre-montane forest
Montano bajo	1,300-2,000 m asl	Lower montane forest
Montano	2,000-2,900 m asl	Montane cloud forest
Montano alto	2,900-3,600 m asl	Upper montane forest

The montane forest zones described here represent a simplification of the gradational vegetation change which occurs with increasing altitude. In reality the vegetation in this heterogeneous and dynamic landscape is controlled not only by environmental drivers associated with altitude but by the interaction of a plethora of biotic and abiotic drivers, contributing to the complexity of species distributions across the Andes. To characterise the vegetation zones a review of the literature describing the broad species compositions was undertaken to provide a representation of the key plant morphological and vegetation compositional characteristics.

2.2.3.3.1 Pre-montane forest

The pre-montane forest (600-1300 m asl) represents the transition from the lowland Amazonian rainforest (Napo moist forest ecoregion) to the tropical montane forests of the eastern Andean flank (eastern cordillera real montane forest ecoregion). As such the vegetation within this zone represents an amalgamation of lowland and montane forest taxa. The forest canopy can reach a height of 40 m and is floristically similar to that of the lowlands, with Fabaceae, Moraceae and Arecaeae the most diverse tree families and Bignoniaceae the largest group of lianas (Webster, 1995). However, families more common within the montane environment such as Melastomataceae and Piperaceae become more

prevalent within this zone (Webster, 1995), with few lowland species exceed the upper limit of 1300 m asl (Sierra, 1999).

2.2.3.3.2 Lower montane forest

Lower montane forest occurs between 1300-2000 m asl and sees a distinct change in forests structure from one dominated by lianas to one covered in epiphytic Araceae, Bromeliaceae, Orchidaceae and ferns. Forest canopy height reaches 25-30 m, but lacks the emergent layer seen within the lowland forest (Sierra, 1999). Taxa indicative of the lowlands, from families such as Bombacaceae and Myristicaceae disappear, and are replaced by a characteristic Andean vegetation assemblage. Taxa common in the lower montane forest include; *Cecropia* (Urticaceae), *Elaegia* (Rubiaceae), *Ficus* (Moraceae), *Geonoma* (Arecaceae), *Hedyosmum* (Chloranthaceae), *Miconia* (Melastomataceae), *Ocotea* (Lauraceae), *Piper* (Piperaceae), *Sapium* (Euphorbiaceae).

2.2.3.3.3 Montane cloud forest

Montane cloud forests (2000-2900 m asl) are characterised by their abundant epiphytes especially Bromeliaceae, Orchidaceae and ferns, with almost every surface covered in a layer of bryophytes and lichens (Harling, 1979). Trees become more stunted in height, rarely exceeding 20 m, with leaf area decreasing with increased altitude and trees beginning to display gnarled trunks and knotted branches (Webster, 1995; Neill, 1999b). The steep and unstable slopes of the montane cloud forest give rise to a dense undergrowth growing on fallen, rotting trees, often dominated by the palm *Geonoma* or grass *Chusquea* on the more open slopes (Gentry, 1995; Valencia, 1995). Pioneer species such as *Cecropia* are prevalent in areas of forest disturbance and increased human impact, while monospecific stand of *Alnus* can occur after landslides (Guariguata & Ostertag, 2001). Taxa common in the montane cloud forest include; *Alchornea* (Euphorbiaceae), *Alnus* (Betulaceae), *Barnadesia* (Asteraceae), *Cecropia* (Urticaceae), *Chusquea* (Poaceae), *Inga* (Fabaceae), *Ficus* (Moraceae), *Geonoma* (Arecaceae), *Gunnera* (Gunneraceae), *Hedyosmum* (Chloranthaceae), *Hieronyma* (Phyllanthaceae), *Miconia* (Melastomataceae), *Myrcianthes* (Myrtaceae), *Ocotea* (Lauraceae), *Piper* (Piperaceae), *Weinmannia* (Cunoniaceae).

2.2.3.3.4 Upper montane forest

Trees in the upper montane forest (2900-3600 m asl), rarely exceeding 20 m in height, frequently have gnarled trunks and knotted branches and consist of taxa with smaller leaf areas than those at lower elevations, e.g. *Weinmannia* and *Polylepis* (Webster, 1995). Epiphytic Bromeliaceae, Orchidaceae and ferns are still common within the lower part of this zone but decrease approaching the upper tree line, however surfaces remain covered in a layer of bryophytes and lichens. This vegetation zone includes an ecotone above ~ 3200 m asl where montane forest begins to transition into the high elevation páramo, this subalpine forest or 'Ceja Andina' (eyebrow forest) positioned above the permanent cloud cover, sees an increase in taxa such as *Hypericum*, *Oreopanax*, *Miconia* and characteristic patches of *Polylepis* (Webster, 1995; Neill, 1999b). Taxa common in the upper montane forest include; *Alnus* (Betulaceae), *Dixonia* (Dixonaceae), *Gynoxys* (Asteraceae), *Hedyosmum* (Chloranthaceae), *Hesperomeles* (Rubiaceae), *Ilex* (Aquifoliaceae), *Miconia* (Melastomataceae), *Oreopanax* (Araliaceae), *Piper* (Piperaceae), *Podocarpus* (Podocarpaceae), *Vallea* (Elaeocarpaceae).

2.2.3.4 Quijos Canton vegetation

The locations sampled within this study are situated within the 'cloud forest' vegetation zone according to the classification of Sierra (1999). Today the vegetation within this zone is dominated by a mosaic of secondary disturbed forest and open pastures along the edges of the Río Quijos and Río Cosanga.

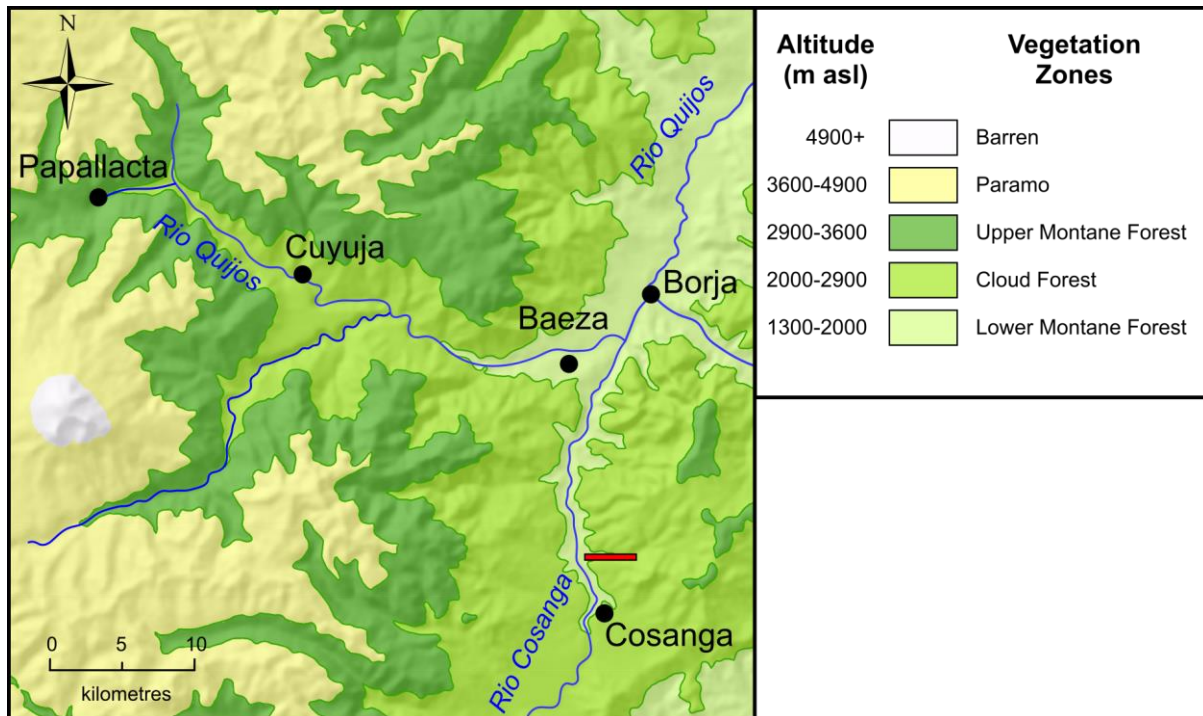


Figure 2.7 Vegetation zones and their altitudinal extent used within this study based on those of Sierra (1999). Red line indicate modern pollen transect at Erazo (Cárdenas et al., 2014).

Surveys of suspected ‘intact’ vegetation within the Quijos Canton are limited. A survey near the town of Baeza (1915 m asl) of a 1 hectare plot, suggested that the forest had been undisturbed for at least 60 years, displaying a vegetation assemblage consisting primarily of Arecaceae, Lauraceae, Lamiaceae, Moraceae and Fabaceae with an understory dominated by the palm *Geonoma* (Valencia, 1995). While a survey from a suspected intact plot at Borja within the lower montane forest (1710m asl) was characterised by the families Lauraceae, Moraceae, Rubiaceae and Fabaceae (Grubb et al., 1963). Few modern pollen-vegetation studies have been undertaken from within the northern Andes (Hansen et al., 1984; Melief, 1985; Bush, 1991; Marchant et al., 2001; Weng et al., 2004b; Rull, 2006), and only four from the Andes of Ecuador (Bush et al., 1990; Moscol-Olivera et al., 2009; Niemann et al., 2010; Cárdenas et al., 2014). The modern pollen analysis undertaken by Cárdenas et al. (2014), recorded pollen through the lower montane forest - cloud forest transition near the town of Cosanga (Fig. 2.8). The altitudinal transect was undertaken through ‘human disturbed’ and what is suggested to be ‘undisturbed dense-closed woodland’ from 1895-2220 m asl. However, the pollen spectra shows an over representation of the taxa *Cecropia* (~ 38-64 % of the pollen sum) within the ‘undisturbed dense-closed woodland’. *Cecropia* is a pioneer

taxa, that rapidly colonizes disturbed areas and is a primary component in secondary forests (Colinvaux et al., 1999), suggesting that these possible fragments of intact forest are unlikely to be undisturbed. Today clearance and cultivation of all but the steepest slopes, themselves victims of frequent disturbance by landslides, would suggest that intact montane cloud forest communities no longer exist with the Quijos region and that even the most dense and inaccessible forest fragments likely represent secondary forest.

2.3 Sample locations

The overarching goal of this study is to understand the response of tropical montane forest vegetation to changing human impact through time. Therefore, a study region was identified that offered the greatest likelihood of containing evidence of persistent human occupation within the montane forest from the pre-Hispanic period, through European colonialization to the modern day. The Quijos Valley met these historical requirements, being the primary trade route from the historically important city of Quito in the high Andes to the Amazonian lowlands. Preliminary archaeological evidence from 1970 (Porrás, 1975) followed up in 2008 (Cuéllar, 2009), recorded an abundance of pottery shards and evidence of pre-Hispanic indigenous populations near the town of Baeza (Fig. 2.8) and historical documentation from the period of Spanish arrival contained unusually detailed accounts of indigenous populations and polities.

Patricia Mothes, head of volcanology at the Instituto Geofísico of the Escuela Politécnica Nacional in Quito, Ecuador and has spent much of the last 25 years characterising the volcanic history of northern Andes, within the context of mitigating the risk of earthquakes and volcanic eruptions to the people of Ecuador. During 2006, Mothes located a small lake situated within the Quijos Valley at Hacienda Huila near a newly installed seismic station, while researching the Antisana volcano (Hall et al., 2017). Later in 2008 Mothes also identified a sedimentary exposure near the town of Cosanga, consisting of interbedded volcanic tephra layers and organic sediments which were hypothesised to have been deposited sometime during the Pleistocene. Mothes experience working in the Andes understood the potential of these sites to better understand the geological and ecological history of the region, and in collaboration with William Gosling (The Open University /

University of Amsterdam) sought to sample and analyse these sediments. These two locations, correspond to the Lake Huila sedimentary core (from here on referred to as Huila) and the Cosanga-Vinillos sedimentary section (from here on referred to as Vinillos). In 2012 Vinillos was sampled by a team from The Open University headed by William Gosling and consisting of Encarni Montoya, Hayley Keen, Frazer Matthews-Bird and James Malley. In 2013 a return trip to the Quijos Valley the group from The Open University this time headed by Encarni Montoya and included William Gosling and Nicholas Loughlin cored Huila and an adjacent bog, and collected modern samples from a number of secondary forest fragments in the Quijos and Cosanga valleys (Fig. 2.8). Details of the samples collected in the field and analysed are summarized in Table 2.2.

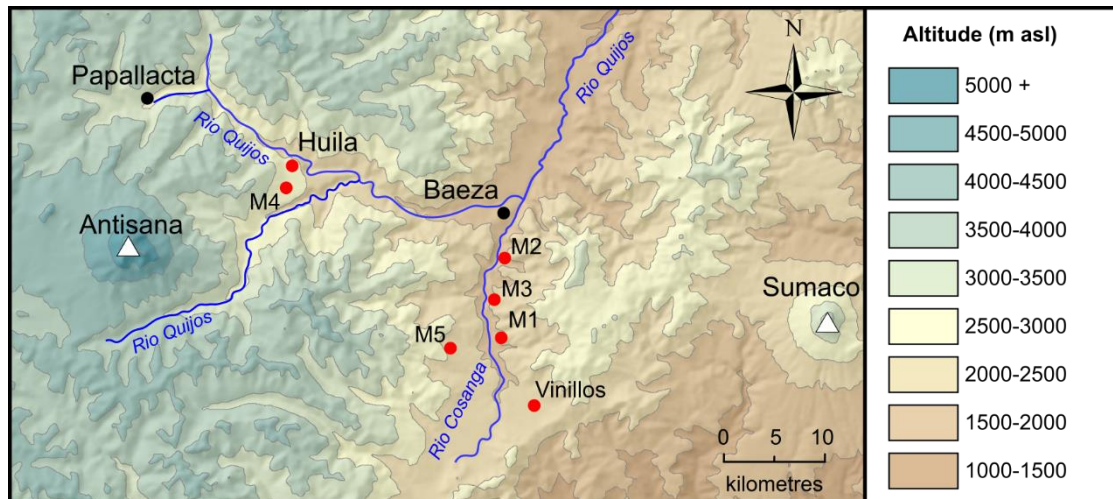


Figure 2.8 Location of samples site. Topography of the Quijos and Consanga valleys with contour lines at 500 m intervals. Red circles indicate samples sites (Huila, Vinillos and modern (M) samples), black circles indicate towns and white triangles volcanic peaks.

2.3.1 Huila

Huila (00° 25.405' S, 78° 01.075' W; 2608 m asl) is a small lake located at Hacienda (*Farm*) Huila (occasionally spelled as *Guila*) within the Quijos Canton in the province of Napo, Ecuador. The lake is located at the base of the Antisana volcano, on an undulating plateau, or terrace, formed by andesitic lavas that flowed from Antisana's central edifice approximately 210 ka ago (Hall et al., 2017). The lake is situated at the confluence of two tributaries of the Río Quijos (Fig. 2.9 A). The adjacent village of Cuyuja is situated

equidistance between the towns of Papallacta (3300 m asl) and Baeza (1915 m asl) within the Quijos Valley through which runs the primary road (28C) connecting the Andes of northern Ecuador to the Amazonian region.

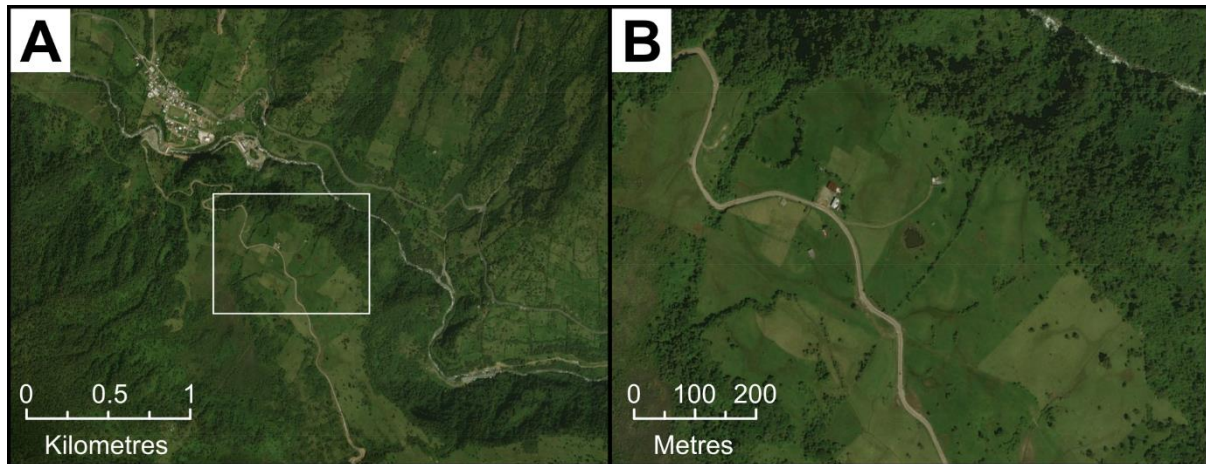


Figure 2.9 Aerial images of region around Huila. A) Quijos Valley with location of Huila in respect to the Río Quijos and the village of Cuyuja, B) Hacienda Huila and the position of Lake Huila with the pasture.

The land around the lake is a mosaic of open pastures and secondary forest, containing cattle and horses, there appears to be no cultivation of crops around the lake today (Fig 2.9 B). Vegetation close to the lake is dominated by grasses and sedges and includes herbaceous taxa from families such as Asteraceae, Apiaceae, Lamiaceae and Verbenaceae. Ferns are common, occurring in the wetter areas of the open landscape. Occasional lone trees or lines of individuals are used to separate fields and are predominantly of the families Melastomataceae and Lauraceae. The trees are rarely above 6 metres in height and are consistently blanketed in epiphytic Bromeliaceae, Araceae, lichens and bryophytes. A large tree stump of ca. 150 cm in diameter (considerably bigger than any extant tree) is located near the western edge of the lake.

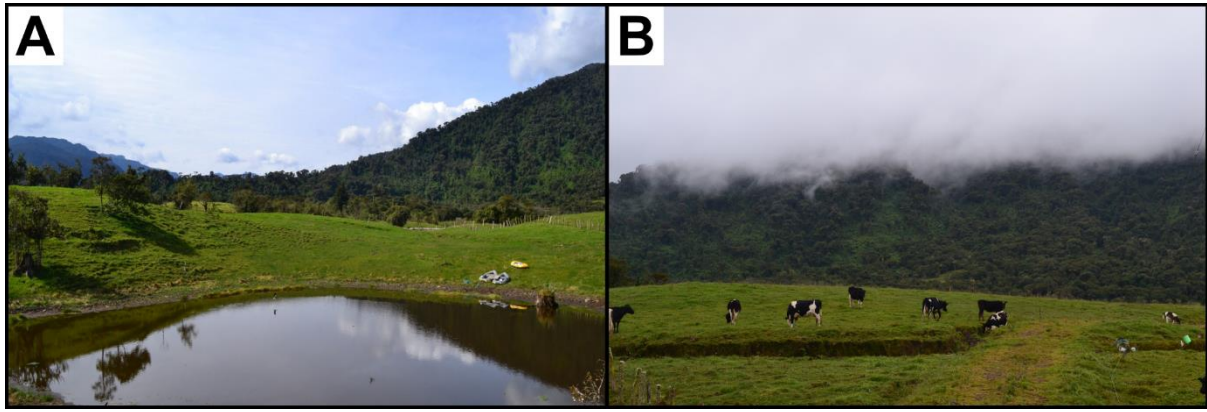


Figure 2.10 Huila study area. A) Lake Huila situated within its confined basin. B) Open pasture around Huila, with cloud covered montane forest present on the steeper slopes.

Lake Huila (the water body) is approximately 35 m in diameter and dips shallowly to its deepest point of ca. 1.17 m at its centre (Fig 2.10). Based on local knowledge the lake has not been known to dry up completely during living memory. The lake is enclosed within a small drainage basin of ca. 7000 m², with no obvious source or output, as such it is suspected that surface water runoff resupplies the lake and drainage occurs through seepage. Slopes surrounding the lake range from 2°-25°, however the basin topography means that the depth of Huila cannot exceed ca. 4 m due to the height of the basin to the north (Fig 2.11). The hollow that the lake is situated in is one of several similar features at Hacienda Huila, this includes the nearby bog which is located approximately 120 m to the north-west at an elevation approximately 15 m lower than that of the lake.

Huila was successfully sampled in November 2013 using a Livingstone corer with a Colinvaux-Vohnout piston modification (Livingstone, 1955; Colinvaux et al., 1999). Coring took place from a floating platform attached to two anchored boats. Individual core lengths of up to 1 m were recovered at a time. Samples were stored within their aluminium tubes for transportation back to the laboratory (The Open University) and kept in a cold room at 4°C until required. Overlapping sediment cores were taken from the centre of Huila, the longest core (Huila-E) reached a total depth of 2.09 m and was used for analysis. Bedrock was not reached during coring.

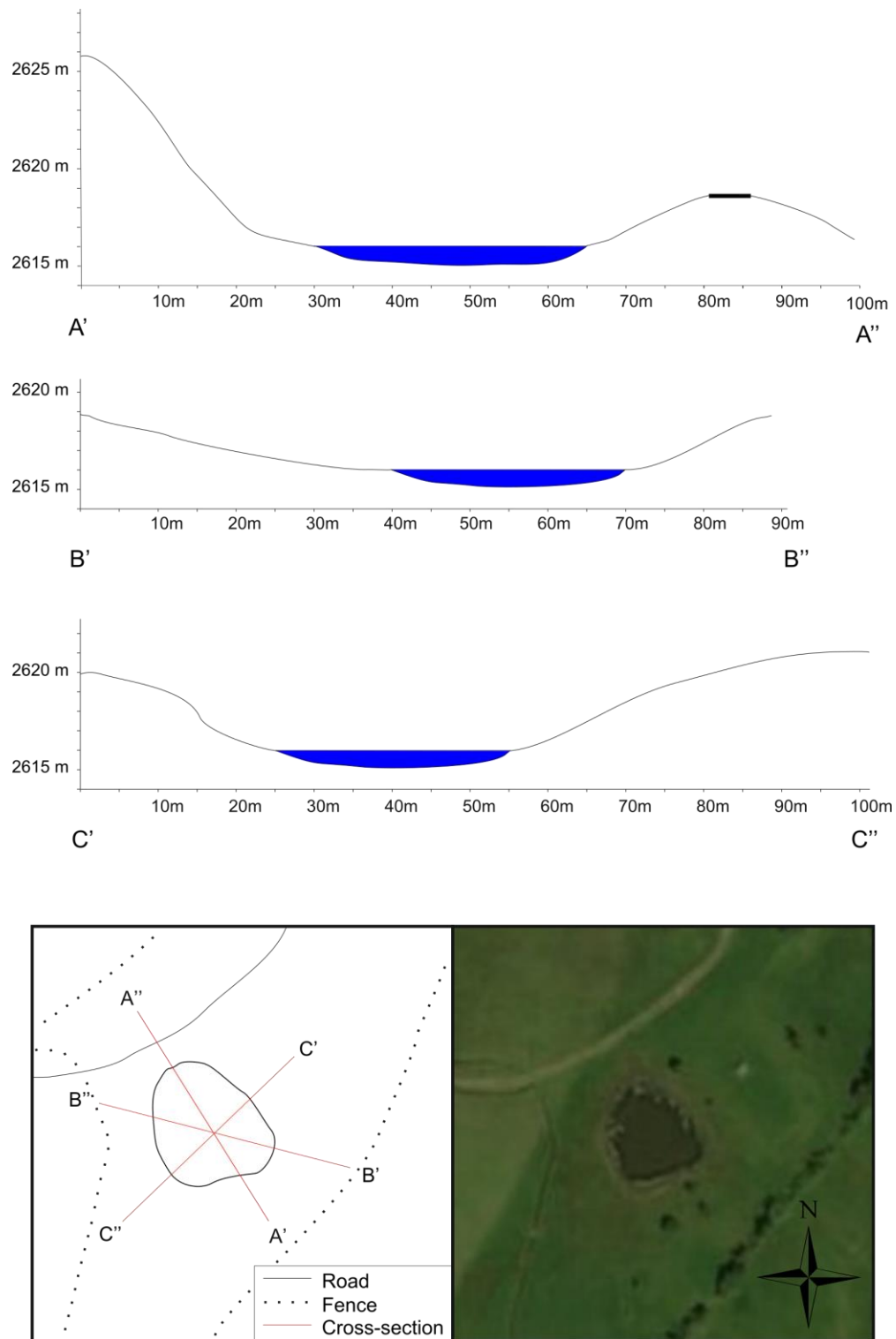


Figure 2.11 Three cross-sections through the Huila basin. Measurement where taken using a GPS, 50 m tape measure and a compass-clinometer to determine the position, size and shape of the basin. Lake depth and profile was measure using a measuring stick.

The Huila core (Huila-E) is composed of 25 cm of dark brown to black, clays and peats, and 155 cm of light brown sandy clay containing a 26 cm light grey volcanic tephra layer (Fig. 2.12). A total of three wood fragments were recovered from the core between 12-20 cm in depth and a small pottery sherd at 42 cm. Initial analysis of the Huila core indicated a paucity of palynomorphs below the tephra layer, as such attention was concentrated primarily on the upper portion (49 cm) of the core.

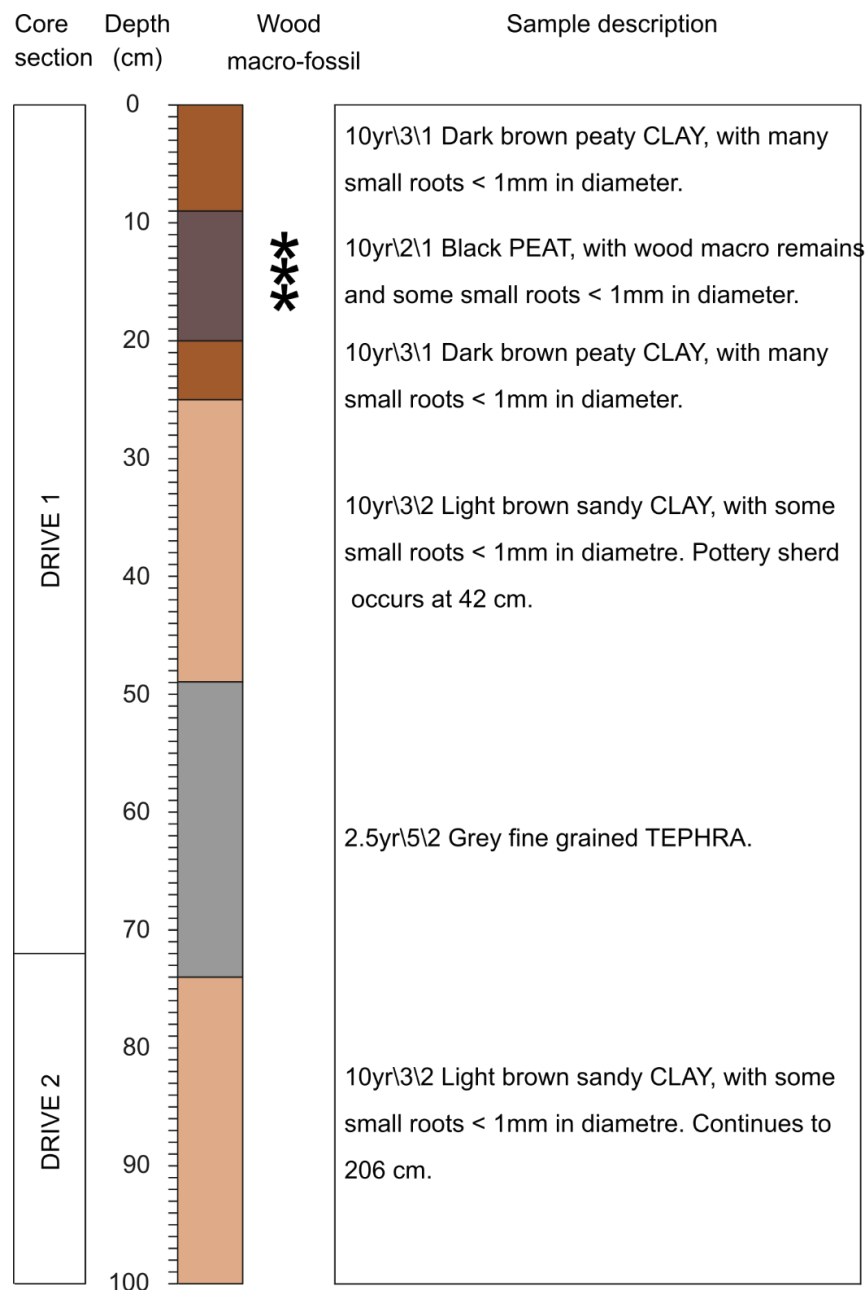


Figure 2.12 Upper 1 m of the 2.09 m Huila core. The upper 1 m of the Huila core was the target of analysis. The remainder of the core consisted of the same material found below the tephra layer and preliminary analysis indicated that it was essentially barren of pollen (< 10,000 grains per cm³).

2.3.2 Vinillos

Vinillos (00° 36.047 S, 77° 50.814 W; 2090 m asl) is an exposed cliff section located 3 km south-east of the town of Cosanga within the Quijos Canton in the province of Napo, Ecuador (Fig 2.13). The section is situated approximately 150 m above and 3 km to the east of the Río Cosanga within a road cutting along the Troncal Amazónica (E45). The Cosanga Valley occurs between the eastern Andean flank and the region referred to as the Napo uplift which incorporates the Sumaco volcano.

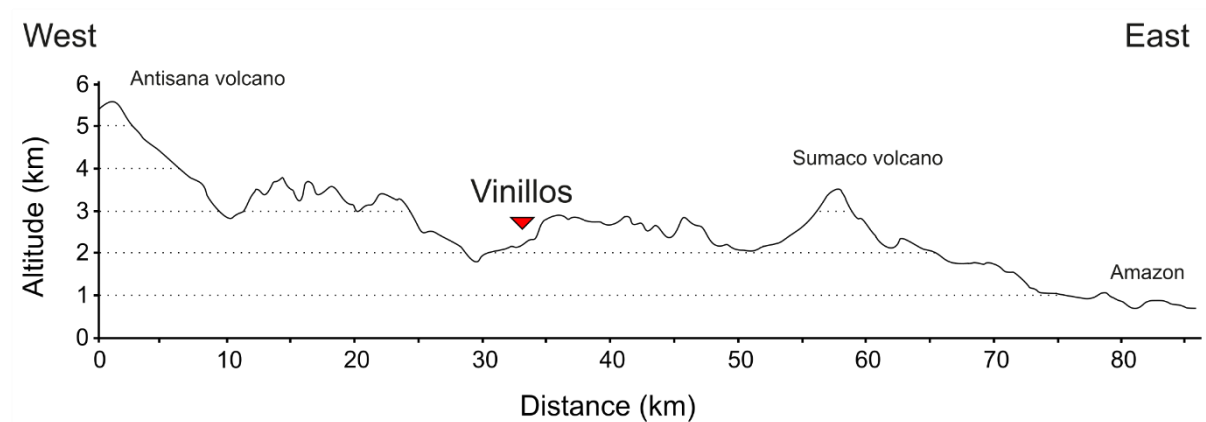


Figure 2.13 Cross section through the Cosanga Valley from the Antisana volcano through the Vinillos section and Sumaco volcano.

Anthropogenic disturbance and deforestation around Vinillos means that the modern vegetation is primarily open pasture, fields used for cultivation, primarily maize (*Zea mays*) and bananas (*Musa acuminata*), or secondary forest. The forest is characterised by trees from the families Lauraceae, Rubiaceae, Urtiaceae, Melastomataceae and Moraceae, and are blanketed in epiphytic Bromeliaceae, Araceae, lichens and bryophytes. Vegetation directly above and surrounding the exposed sediments include characteristic disturbance indicators such as *Cecropia* (Urticaceae), *Chusquea* (Poaceae) and *Gunnera* (Gunneraceae). Indeed, between sampling of the section in September 2012 and returning in November 2013 the formally cleared slope had been colonised by a community of pioneer taxa consisting of predominantly *Gunnera* (Gunneraceae), *Chusquea* (Poaceae) and ferns (Fig 2.14).

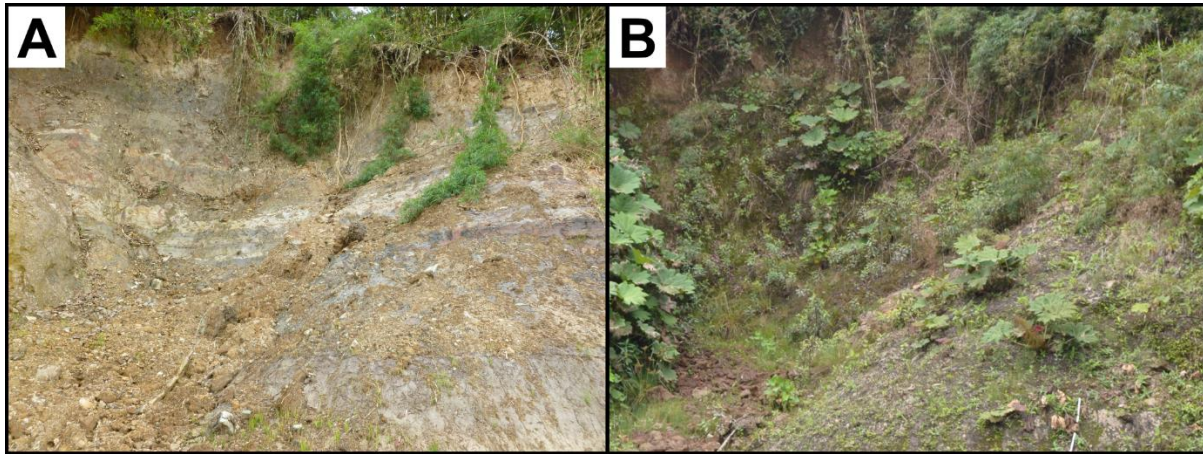


Figure 2.14 The Vinillos section. A) Section during sampling of the sequence in 2012. B) Section one year later in 2013.

Vinillos was sampled through two sections referred to as section A (upper section) and section B (lower section) (Figs 2.15 and 2.16). Prior to sampling the section was cleaned and vegetation removed. Sediment samples were taken every 5 cm through the organic layers beginning at the top of the section and constituted a 1 cm deep cutting. Discrete bulk samples were taken from each of the four volcanic ash layers. Samples were taken with a knife which was cleaned after each sample. The recovered material was double bagged and all pertinent information recorded. Samples were transported to the laboratory at The Open University where they were stored in a cold room (4°C) until required. The Vinillos sediments display numerous interbedded volcanic ash layers (tephra) and dark, organic rich peats and clay layers. Large wood macro-fossils (100 mm diameter by 300 mm long) were recovered from two of the organic layers during sampling. A light brown sand layer separating the two sections was not sampled.

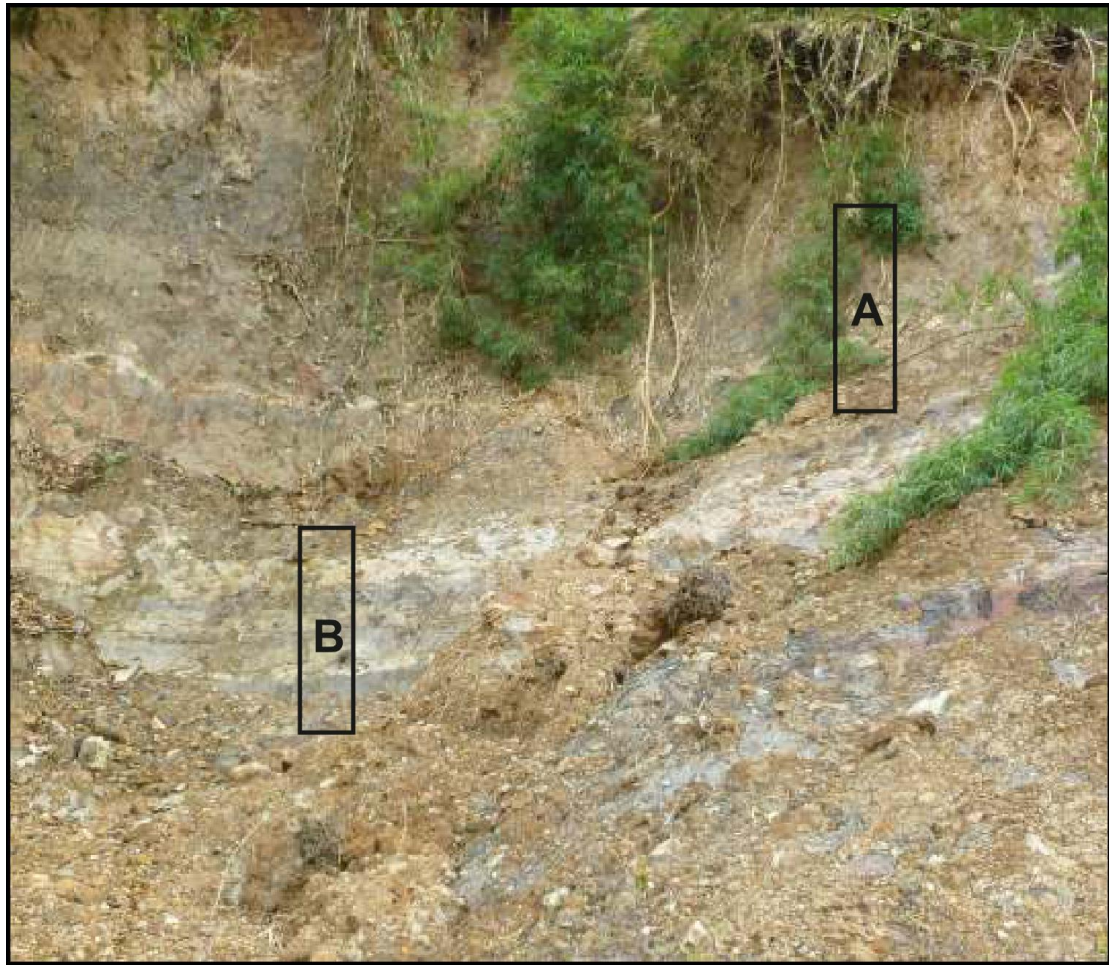


Figure 2.15 Vinillos profile. Sampling over two sections A (1.34 m) and B (1.84 m).

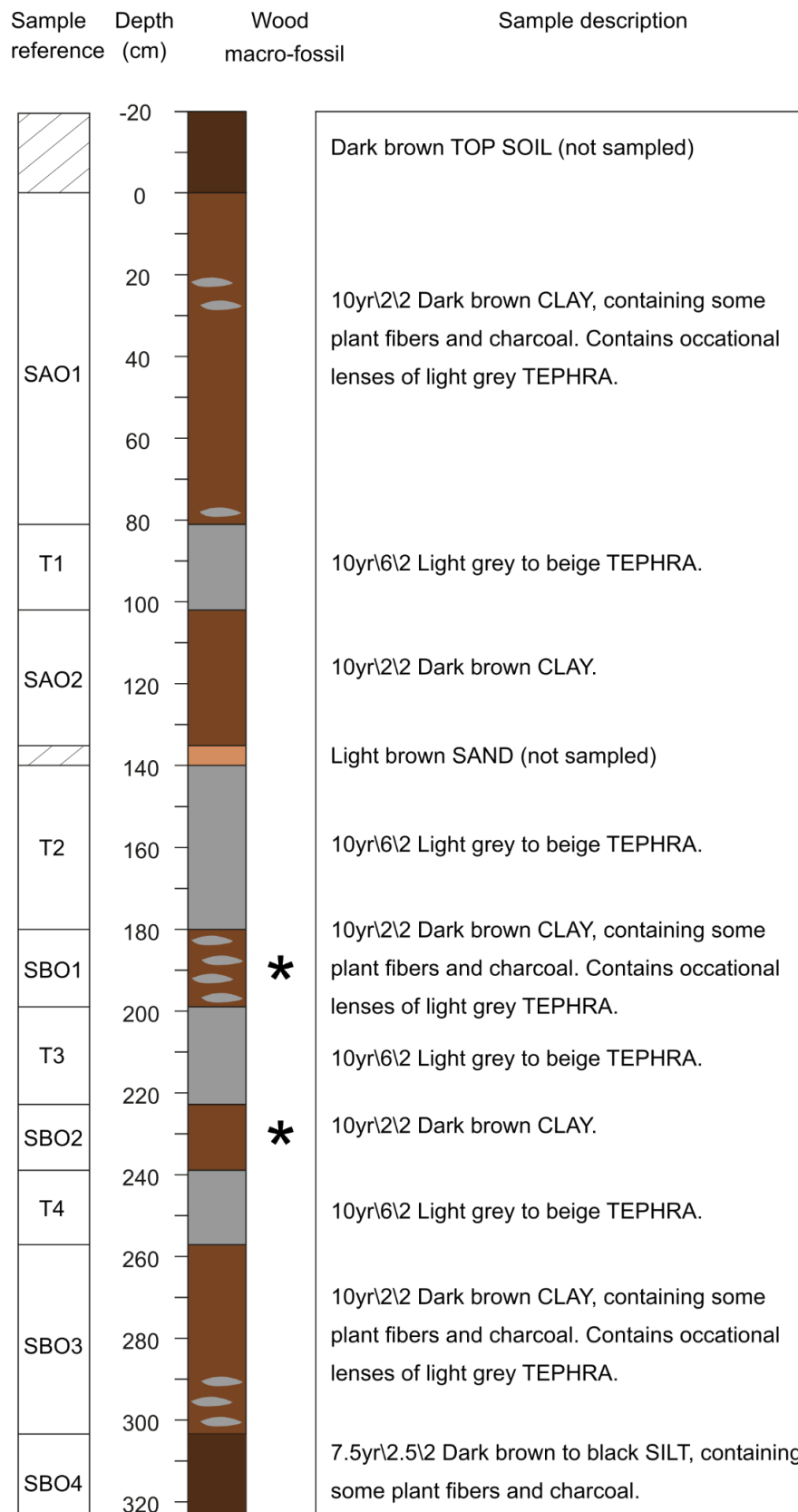


Figure 2.16 The Vinillos section profile with descriptions of sediment. A Munsell colour chart was used to record sediment colour. Asterisks (*) indicate location of wood macro-fossils recovered from the outcrop.

2.3.3 Modern sample 1

Modern sample 1 (M1) (00° 32.930 S, 77° 52.655 S; 1925 m asl) was a moss polster taken from ground level in an isolated section of closed canopy secondary forest. The forest fragment is approximately 200m from a road and surrounded by open pastures. Canopy trees were predominantly Melastomataceae, Lauraceae, *Weinmannia*, Moraceae, Urticaceae and Rubiaceae. Epiphytic bromeliads were common within the crowns, with ferns and Araceae near the base of the trunk. Bryophytes and lichens covered trunks, branches and older leaves. The herbaceous layer was open and contained predominantly grasses and ferns.

2.3.4 Modern sample 2

Modern sample 2 (M2) (00° 30.260 S, 77° 52.598 W; 1801 m asl) was a moss polster taken at ground level in an isolated section of closed canopy riparian forest. The forest fragment is approximately 10 m from the river (Río Cosanga) and next to abandoned field dominated by Poaceae. Canopy trees and shrubs were predominantly Melastomataceae, Lauraceae, *Clethra*, Moraceae, Urticaceae and tree ferns. Epiphytic bromeliads, ferns and Araceae are common, with bryophytes and lichens covered trunks and branches. The herbaceous layer was open and composed of decaying leaf litter and ferns.

2.3.5 Modern sample 3

Modern sample 3 (M3) (00° 32.278 S, 77° 52.624 W; 1798 m asl) was a damp surface soil sample taken from ground level in an isolated section of closed canopy riparian forest. The forest fragment is approximately 10 m from the river (Río Cosanga), 200 m from the road and surrounded by open pastures. Canopy trees are predominantly Melastomataceae, Lauraceae, *Clethra* and Asteraceae. Epiphytic bromeliads are common within the crowns, with ferns and Araceae near the base of the trunk. Bryophytes and lichens covered trunks, branches and older leaves. The herbaceous layer is characterised by members of the families Rosaceae, Apiaceae, Asteraceae, Poaceae, Juncaceae and by ferns.

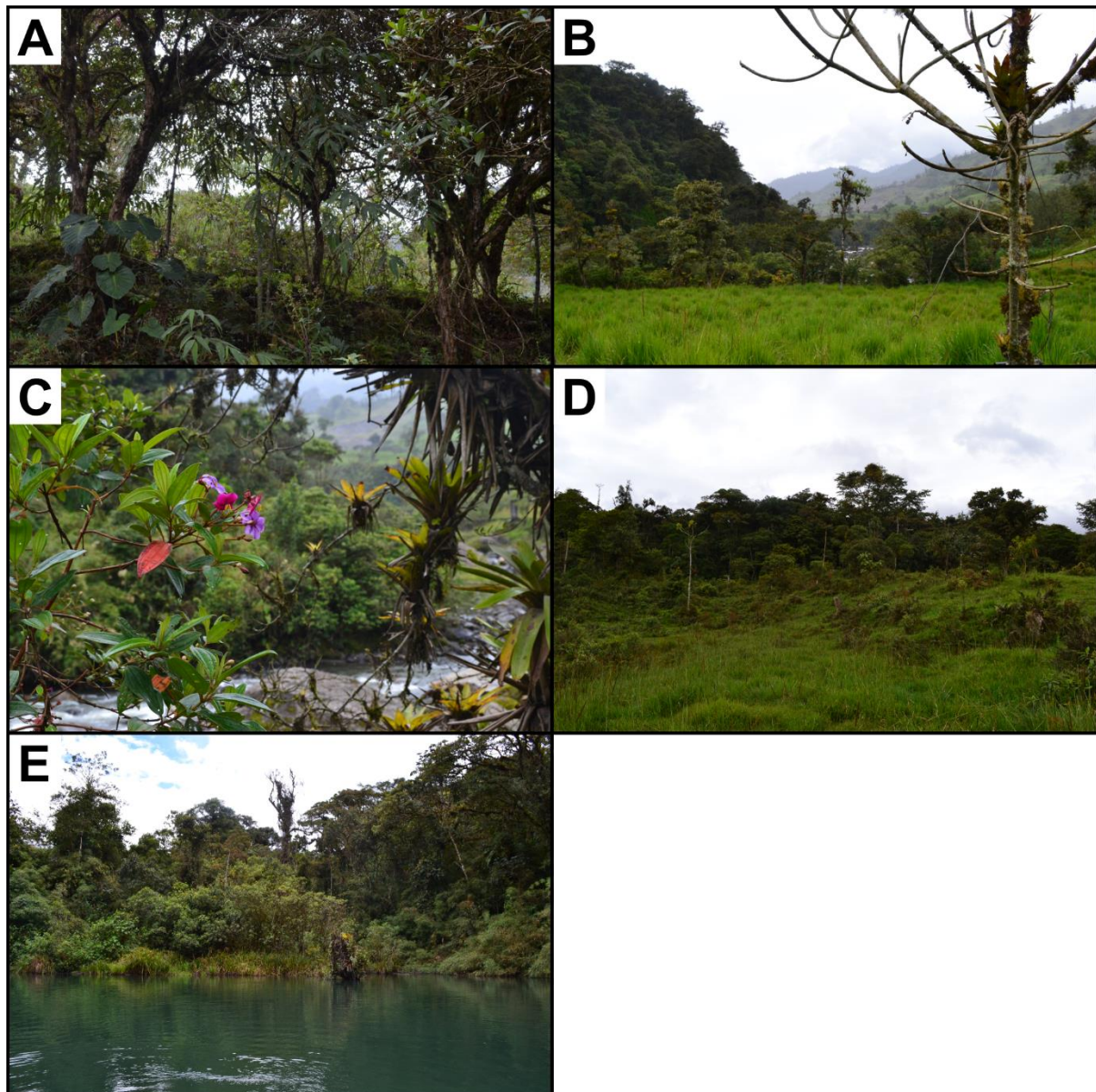


Figure 2.17 Location of modern sites. A) M1, B) M2, C) M3, D) M4, E) M5 (Lake Erazo).

2.3.6 Modern sample 4

Modern sample 4 (M4) (00° 26.608 S, 78° 00.431 W; 2611 m asl) is a damp surface soil sample taken on the edge of secondary forest approximately 1 km south of Lake Huila. The sample was taken approximately 10 m from the road and surrounded fields that are used for cattle farming. A large scale earthworks and deforestation for a hydroelectric plant were ongoing in the general area at the time of sampling. Canopy trees consist of large (> 10 m) Lauraceae, Moraceae, *Weinmannia*, *Hedyosmum* and *Cecropia*. Epiphytic bromeliads, ferns and Araceae cover the larger trees, with bryophytes and lichens covering trunks, branches

and older leaves. Ground level vegetation consists primarily of ferns and the bamboo *Chusquea*.

2.3.7 Modern sample 5

Modern sample 5 (M5; Lake Erazo) (00° 34.127 S, 77° 53.970 W; 2306 m asl) is jet black highly organic clay taken from a lake sediment surface sample (2 cm depth), recovered using a Livingstone corer (see Huila sampling method). Lake Erazo is approximately 40 m in diameter and has a maximum depth of 3.1 m, which slopes gently upwards from the centre. Dense secondary forest (Fig 2.17E), consisting of a wide range of mature canopy trees and shrubs (some exceeding 10 m in height) from the families Lauraceae, Melastomataceae, Rubiaceae, Moraceae, Arecaceae and Urticaceae surround the lake. Grasses (predominantly *Chusquea*) and substantial tree stumps covered in epiphytes occur at the lake edge. Cleared pastures and cultivated fields are located approximately 200 m down slope from the lake. Inflow is located in the western corner of the lake flowing over a gravel bed stream, with an outflow to the east (downslope) flowing into a narrow gully. The lake appears to be located within a blocked valley, but no obvious evidence of its formation was observed at the time of sampling. Subsequent coring of the lake in 2015 by William Gosling recovered ca. 2 m of sediment that was radiocarbon dated to post-1950, suggesting that the formation of the lake and its sediments are associated with a recent landslide event.

Table 2.2 Summary of the samples collected in the field and the number subsampled for analysis. Details of sample locations and characteristics can be found within the Appendix (Table 8.1).

Location	Sediment examined	Radiometric dating	Pollen	NPPs	Micro-charcoal	Macro-charcoal	LOI	Geo-chemistry	Chapters discussed
Huila	128 cm core	11 AMS	28	26	26	50	23	1	3 & 5
Vinillos	325 cm cliff	2 AMS	26	26	29	33	50	4	3, 4 & 5
Various	5 surface samples	0 (Modern)	5	5	-	-	-	-	5

Chapter 3

3 Identifying environmental drivers of fungal non-pollen palynomorphs in the montane forest of the eastern Andean flank, Ecuador.

3.1 Overview

This chapter uses a novel approach to non-pollen palynomorph analysis to better understanding the response of montane forests to ecosystem drivers. The chapter is based on a manuscript published in the Livingston and Colinvaux: Special Issue of Quaternary Research.

Loughlin, N.J.D., Gosling, W.D., Montoya, E. (2018) Identifying environmental drivers of fungal non-pollen palynomorphs in the montane forest of the eastern Andean flank, Ecuador. *Quaternary Research*. 89(1): 119-133.

3.2 Abstract

Samples taken from sedimentary archives indicate that fungal non-pollen palynomorphs (NPPs) can be used to provide information on forest cover, fire regime and depositional environment in the eastern Andean flank montane forest of Ecuador. Within the 52 samples examined, 54 fungal NPP morphotypes are reported, of which 25 were found to be previously undescribed. Examination of fungal NPPs over a gradient of forest cover (2-64 %) revealed three distinct assemblages: (i) low (< 8 %) forest cover *Neurospora*, IBB-16, HdV-201, OU-102 and OU-110 indicative of an open degraded landscape, (ii) medium (8-32 %) forest cover *Cercophora*-type 1, *Xylariaceae*, *Rosellinia*-type, *Kretzschmaria deusta*, *Amphirosellinia*, *Sporormiella* and *Glomus* suggestive of a forested landscape disturbed by herbivores and soil erosion, and (iii) high (32-63 %) forest cover *Anthostomella fuegiana*, OU-5, OU-101, OU-108 and OU-120. Environmental variables for forest cover (forest pollen), available moisture (aquatic remains), regional fire regime (micro-charcoal), and sediment composition (organic carbon) were found to explain ca. 40 % of the variance in the fungal NPP dataset. Fire was found to be the primary control on fungal NPP assemblage composition with available moisture and sediment composition the next most important factors.

3.3 Introduction

Estimates of global fungal diversity range from 1.5 - 5.1 million species (Blackwell, 2011; Hawksworth, 2012) with the greatest diversity found in tropical lowland and montane environments (Tedersoo et al., 2014). Fungi perform a vital function in terrestrial ecosystems as symbionts and decomposers of vegetation. Due to this role a close relationship exists between plant and fungal communities (Hooper et al., 2000; Peay et al., 2013). Environmental drivers, including climate, fire regime, edaphic factors, and spatial distribution, play a role in fungal community composition (Tedersoo et al., 2014). The link between fungal community and environment allows fungal remains (ascospores, conidia, chlamydospores) preserved in sedimentary archives to be used as a proxy in reconstructing palaeoenvironments (van Geel, 1972).

Non-pollen palynomorphs (NPPs), which include fungal remains, zoological remains, plant fragments, and algae, were first utilised to complement fossil pollen in reconstructing

palaeoenvironmental records from northern-European peat bogs (van Geel, 1972, 1976, 1978, van Geel et al., 1981, 1983; Kuhry, 1985). Combining NPPs with fossil pollen records has allowed new insight into past ecosystem functions to be gained and consequently resulted in a more complete understanding of how, and why, ecosystems develop and change through time. Fungal NPPs have been used successfully to establish past trends of anthropogenic impact (van Geel et al., 2003; López-Sáez & López-Merino, 2007; Williams et al., 2011), provide evidence of herbivore extinctions (Davis, 1987; Gill et al., 2009, 2013), the role of herbivores in shaping landscapes (Davis & Shafer, 2006; Raper & Bush, 2009; Baker et al., 2013, 2016) and past mammalian behaviour (van Geel et al., 2008, 2011). Despite the ability of fungal NPPs to provide unique complimentary information on past environments their use in the Neotropics has been limited due to a paucity of studies (Montoya et al., 2012), and within the Andes their use is restricted to Venezuela (Rull & Vegas-Vilarrúbia, 1998, 1999; Rull et al., 2008; Montoya et al., 2010, 2012) and Colombia (Hooghiemstra, 1984; Kuhry, 1988; Grabandt, 1990).

The generally diverse nature of ecosystems and landscapes in the tropics has long been discussed (Wallace, 1878; MacArthur, 1969; Connell, 1978; Stevens, 1989), and has led to the tropical Andean region being identified as containing some of the most biodiverse ecosystems on the planet (Myers et al., 2000). Within the Andean biodiversity hotspot the increase in species diversity within mid-elevation Andean tropical forests has been the focus of particular attention (Terborgh, 1977; Graham, 1983; Gentry, 1988). The reason for high biodiversity in the Andes has been variously attributed to the regions heterogeneous nature, dynamic environment, and high precipitation (Killeen et al., 2007; Hoorn et al., 2010). However, questions remain unanswered about the long-term ecological and environmental processes operating within these biodiverse Andean forests. The development of fungal NPPs as a proxy within the eastern Andean montane forest provides an opportunity to extract a new type of information on long-term ecological and environmental states and processes from the fossil record.

Recently, modern assemblage-environment calibration data sets for two biological proxies have been constructed for the Andes region: (i) pollen (Rull, 2006; Moscol-Olivera et al., 2009; Flantua et al., 2015), and (ii) chironomids (Matthews-Bird et al., 2016a; Matthews-Bird et al., 2016b). These quantitative methodologies use modern assemblage data and

environmental variables to develop transfer functions with the aim of reconstructing past climatic conditions (Juggins & Birks, 2012). The modern calibration approach could be adapted to qualitatively investigate the autoecology of fungal NPPs along environmental gradients to provide new insight into the principal environmental controls governing specific fungal morphotypes. However, equivalent studies on the eastern Andean flank are hindered by the dynamic nature of the landscape, which limits the number of suitable locations (e.g. lakes, swamps, bogs) within mid-elevation montane forests from which proxies, including fungal remains, can be recovered. Alternative sources of samples, such as surface soil and moss polsters have been variously used to characterise the fungal NPPs of modern environments (Montoya et al., 2010). However, comparisons of NPP assemblages between different sample types (e.g. lake sediments vs. soil samples) is not optimal because of large differences induced by the local signal and limited dispersal potential of many fungal remains; i.e. a strong “sample effect” (Wilmshurst & McGlone, 2005; Montoya et al., 2010).

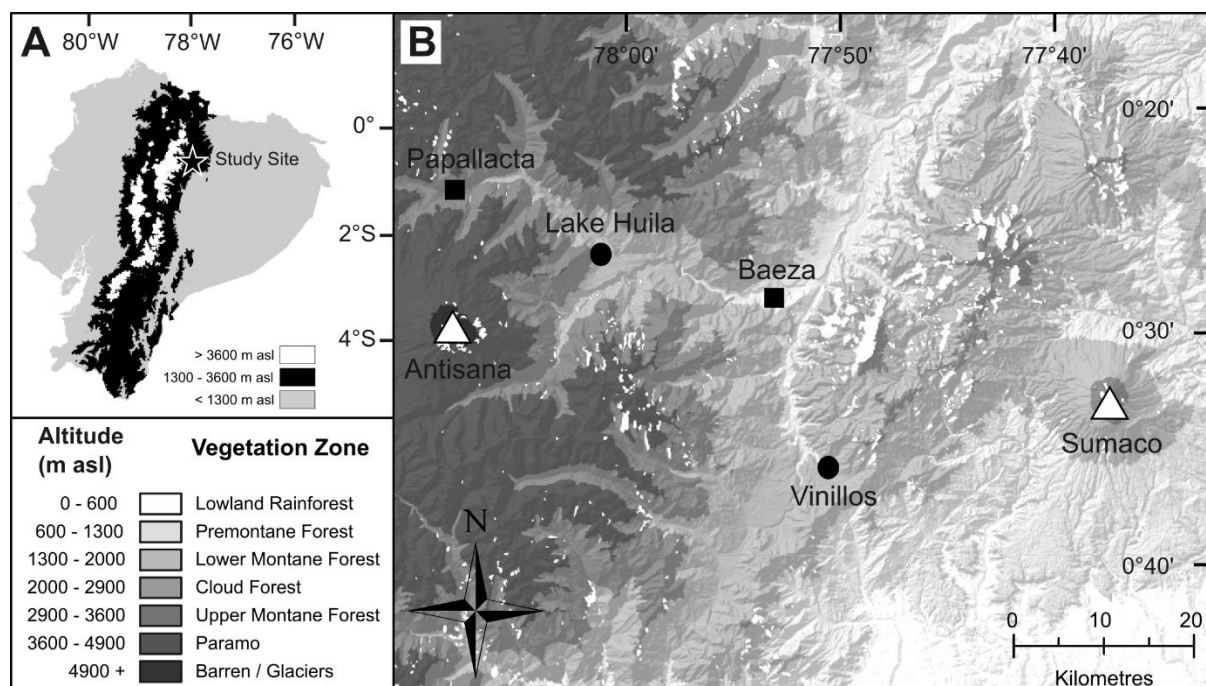


Figure 3.1 Map showing position of study site and sample locations. (A) Map of Ecuador. Regions coloured black indicate an altitude of between 1300-3600 metres above sea level corresponding to Andean montane forest vegetation. (B) Map of study location with altitudinal gradient related to vegetation zones as described in the introduction and corresponding to Sierra (1999). Points indicate sample locations, squares local population centres and triangles volcanic centres.

To overcome the challenge presented by an absence of suitable depositional environments from which to recover a modern calibration data set for NPPs I have developed an alternative approach that relates fungal NPP assemblages to independent environmental proxies in sedimentary archives. In this chapter I use palaeoenvironmental proxies of forest cover (forest pollen), available moisture (aquatic remains), regional fire regime (micro-charcoal), and sediment composition (organic carbon) to provide environmental gradients against which to constrain the autoecological characteristics of fungal NPPs. Using sedimentary archives as a training data set allows us to explore assemblage shifts along longer environmental gradients than would be possible using just modern samples in the Andes. Through using the sedimentary archives I significantly increase the number of samples from the optimal depositional environments (lakes, swamps, and bogs) and reduce the “sample effect” that can bias comparison with the fossil record. Furthermore, using sedimentary archives prior to, and after, the arrival of humans to the continent allows for the exploration of how fungal NPP assemblages developed in landscapes without the influence of people. This novel approach will allow additional information about ecological and environmental processes to be incorporated into future palaeoenvironmental studies.

3.4 The eastern Andean flank, Ecuador

3.4.1 Landscape

The changing topography of the eastern Andean flank is the principle variable controlling vegetation composition, regulating air temperature, precipitation and cloud cover (Harling, 1979; Graham, 2009). Uplift of the Andes began during the Miocene, with the collision of the Nazca and South American plates (Allmendinger et al., 1997), followed by accelerated uplift and widespread volcanic activity during the late Pliocene to early Pleistocene (Coltorti & Ollier, 2000). Throughout the Holocene, Ecuador has experienced a high degree of volcanism with at least 20 active volcanos (Hall et al., 2008). This complex geological history has produced a variety of source rocks that gives rise to the diverse range of soil compositions found within the Andes (Neill, 1999a; Vera, 2013).

3.4.2 Vegetation

Andean montane forests are composed of a narrow band (ca. 30 km) of tropical vegetation covering an altitudinal range of ca. 2300 m (1300-3600 m asl) (Neill, 1999b). Montane forests can be split into three vegetation communities, lower montane forest (1300-2000 m asl), cloud forest (2000-2900 m asl), and upper montane forest (2900-3600 m asl) (Sierra, 1999). Today, the study areas fall within the cloud forest type vegetation community (Fig. 3.1). The cloud forest in this region is composed of a mix of Andean and lowland forest elements including *Alnus* (Betulaceae), Arecaceae, Fabaceae, *Hedyosmum* (Chloranthaceae), Lauraceae, Melastomataceae, Meliaceae, Moraceae, Rubiaceae, Solanaceae and *Weinmannia* (Cunoniaceae) (Harling, 1979; Gentry, 1995; Neill & Palacios, 1997; Neill, 1999b; Valencia et al., 1999). Forest canopy within the cloud forest reaches 15-25 m and trees are covered by abundant epiphytes including mosses, lichens, ferns, Bromeliaceae, Araceae, and Orchidaceae (Webster, 1995; Neill & Palacios, 1997). Today human impact and forest clearance occur within the cloud forest, particularly near river valley floors. Human activity and deforestation is characterised in the vegetation by an increase in herbaceous taxa, disturbance indicators such as *Cecropia* (Urticaceae) and large patches of pioneers such as *Chusquea* (Poaceae) and *Gunnera* (Gunneraceae), which also occurs on steep sided slopes following frequent landslides (Stern, 1993).

3.4.3 Climate

Precipitation on the eastern Andean flank is principally controlled by the South American Summer Monsoon (SASM) (Vuille et al., 2000; Cook, 2009). Mean Annual Precipitation (MAP) varies with altitude with approximately 2500 mm of rainfall per year at 2000 m asl (Neill & Jørgensen, 1999). High levels of orographic rainfall and semi-permanent ground level cloud lead to reduced seasonality and persistent moist conditions (Harling, 1979). Mean Annual Temperatures (MAT) ranges from 16-20 °C at around 2000 m asl (Galeas & Guevara, 2012) with an adiabatic lapse rate of ca. 0.56 °C per 100 m (Bush et al., 2004a). Temperatures remain stable throughout the year, however, diurnal changes in temperature of up to 20 °C can occur at higher elevations, acting as a much more significant control on vegetation distribution than seasonal changes in temperature (Neill & Jørgensen, 1999).

3.5 Study sites and samples

The study area is situated in the Quijos Canton in the Napo Province of Ecuador near the town of Baeza (Fig. 3.1). Two sedimentary archives were recovered from Lake Huila (here on referred to as Huila) and an exposed cliff section near the town of Cosanga (here on referred to as Vinillos). The Huila and Vinillos sediments were selected for development of a fungal NPP training data set because they allowed the fungal NPP assemblages to be constrained against environmental variables when humans were present (Huila), and absent (Vinillos), from the landscape, i.e. the sites are securely radiocarbon dated to before, and after, the arrival of humans in South America ca. 12,000 years ago (Rademaker et al., 2014).

3.5.1 Huila

Huila (00° 25.405' S, 78° 01.075' W) is situated at 2608 m asl on a raised plateau adjacent to the Río Quijos (Fig. 3.1). The lake consists of a shallow (ca. 1.10 m deep) body of water approximately 800 m², within a ca. 4000 m² closed basin, with no obvious inflow. The lake is situated in a cleared pasture used for cattle and horse grazing. The catchment is dominated by Poaceae and Cyperaceae, with the surrounding region consisting primarily of pastures and secondary forest. In 2013 a 2.11 m sediment core was recovered from the centre of the lake from a floating platform using a Colinvaux-Vohnout modified Livingstone piston corer (Livingstone, 1955; Colinvaux et al., 1999). Once recovered the cores were returned to The Open University laboratory intact for storage in a cold room (ca. 4 °C). Radiocarbon dating has shown that the Huila sediments sampled (upper 49 cm) were deposited during the last millennium (Table 3.1.).

3.5.2 Vinillos

The Vinillos section (00° 36.047' S, 77° 50.814' W) is located at 2090 m asl, approximately 3 km south-east of the town of Cosanga (Fig. 3.1) The Vinillos section consists of an outcrop of exposed sediment revealed during the construction of the Troncal Amazónica (E45), a road running parallel to the Río Cosanga. Vinillos is today situated at the boundary between the lower montane forest and cloud forest, with vegetation at the site dominated by disturbance indicators (*Cecropia*, *Gunnera* and *Chusquea*). In 2012 fifty discrete sediment

samples were taken systematically through the dark brown organic beds at 5 cm intervals along with individual bulk samples from four volcanic tephra layers. Samples were placed in zip-lock bags and transported to The Open University to be stored in a cold room (ca. 4 °C). Lithological information was recorded from individual samples in the laboratory. Radiocarbon dating indicates that the Vinillos sediments were deposited prior to ca. 42,000 years ago (Table 3.1).

Table 3.1 Radiocarbon (AMS) ages obtained from palynomorph residues from Huila and Vinillos. The dated sample from Huila is from the base of the sediment analysed, i.e. all the samples presented here are younger than the age of this sample. The dated sample from Vinillos is from the upper part of the sedimentary section, i.e. all the samples presented here are older than the age indicated. Original dates calibrated in OxCal 4.2.4 (Bronk Ramsey et al., 2013) using IntCal13 atmospheric curve (Reimer et al., 2013).

Study site	Laboratory code	Radiocarbon age (years BP $\pm 1\sigma$)	Calibrated radiocarbon age range 2σ (years BP)	Median calibrated radiocarbon age (years BP)
Huila	D-AMS 017471	1,052 \pm 27	971-932	956
Vinillos	SUERC-58952	38,503 \pm 968	43,325-41,885	42,670

3.6 Methods

A total of 52 samples were examined for fungal NPP remains selected from the two sedimentary archives: Huila (26 samples, designated sample codes starting with “H”) and Vinillos (26 samples, designated sample codes starting with “V”). Four independent proxies were also investigated in order to determine specific environmental variables. Three environmental data sets were obtained from the same samples as the NPP assemblages: (i) forest pollen (forest cover), (ii) aquatic remains (available moisture), and (iii) micro-charcoal (regional fire regime). One data set was obtained from additional, equivalent, samples: (i) organic carbon (sediment composition).

3.6.1 Fungal non-pollen palynomorphs

Samples were processed using standard protocols, and included the addition of an exotic marker for the calculation of concentrations (Stockmarr, 1971); University of Lund, Lycopodium tablet batch #124961 containing an average of $12,542 \pm 931$ spores per tablet. Sediment samples of 1 cm³ were sieved at 180 µm and processed using KOH, HCl, HF, and acetolysis (Faegri & Iversen, 1989; Moore et al., 1991). Eleven samples containing high levels of silica (V90, V160, V210, V250, and H31 to 49) were re-sampled and processed using density separation (Bromoform; 2 mol) instead of HF to improve visibility of palynomorphs. Previous studies indicate that samples processed using HF and density separation are directly comparable (Campbell et al., 2016). All sample residues were mounted on glass slides in glycerol and counted on a Nikon Eclipse 50i microscope at 400 x and 1000 x magnification. NPPs remains were counted in conjunction with fossil pollen and are expressed as a percentage relative to the total terrestrial pollen sum; i.e. any taxa with a potential aquatic affinity, such as Cyperaceae and *Myriophyllum*, are excluded from the terrestrial pollen sum. NPPs were counted until a minimum of 300 terrestrial pollen grains had been counted. Deviation from this methodology occurred in sample V5 where fungal spore type HdV-123 was over-represented, accounting for 698.3 % of the pollen sum, here the NPP count was increased until a minimum of 100 non-HdV-123 fungal spores had been counted. Identification of NPPs was undertaken using the available literature (van Geel, 1978; van Geel et al., 1981, 1983, 1989, 2003, 2011; Bakker & van Smeerdijk, 1982; Hooghiemstra, 1984; van Smeerdijk, 1989; Rull & Vegas-Vilarrúbia, 1999; van Geel & Aptroot, 2006; Rull et al., 2008; Cugny et al., 2010; Montoya et al., 2010, 2012; Gelorini et al., 2011; López-Vila et al., 2014) types were recorded and their known ecological affinities described (Appendix A). New NPP morphotypes encountered were assigned a unique code with the designation OU (The Open University) and their morphological characteristics described based on a minimum of five examples (Appendix B). New morphotypes, where fewer than five examples could be found, were not described nor included in the diagrams.

3.6.2 Environmental variables

Four environmental variables were parameterised using independent proxies: (i) forest cover (forest pollen), (ii) available moisture (aquatic remains), (iii) regional fire regime (micro-charcoal), and (iv) sediment composition (organic carbon).

From the complete terrestrial fossil pollen datasets four pollen types (*Alnus*, *Weinmannia*, *Hedyosmum* and Melastomataceae) were selected as representatives of a Andean cloud forest vegetation community based on their occurrence in: (i) modern vegetation surveys (Gentry, 1995; Jørgensen & León-Yáñez, 1999), (ii) modern pollen rain (Weng et al., 2004b; Rull, 2006; Cárdenas et al., 2014), and (iii) late Quaternary sedimentary archives (Hooghiemstra & van der Hammen, 1993; Colinvaux et al., 1997; Urrego et al., 2005; Niemann & Behling, 2008; González-Carranza et al., 2012; Cárdenas et al., 2014). This group of Andean cloud forest pollen taxa are referred to collectively from here on as “forest pollen”.

Aquatic remains consisting of pollen and spores of aquatic taxa (Cyperaceae, *Myriophyllum* and *Isoetes*), algae (*Botryococcus*, *Spirogyra*, *Concentricystis*, *Mougeotia*, *Zygnema*, *Debarya*, HdV-166B and HdV-333), and the remains of aquatic organisms (Chironomidae head capsules, HdV-179 and HdV-353B) were counted in conjunction with the terrestrial pollen. All aquatic remains were combined and expressed as a percentage relative to the total terrestrial pollen sum to provide information on the available moisture.

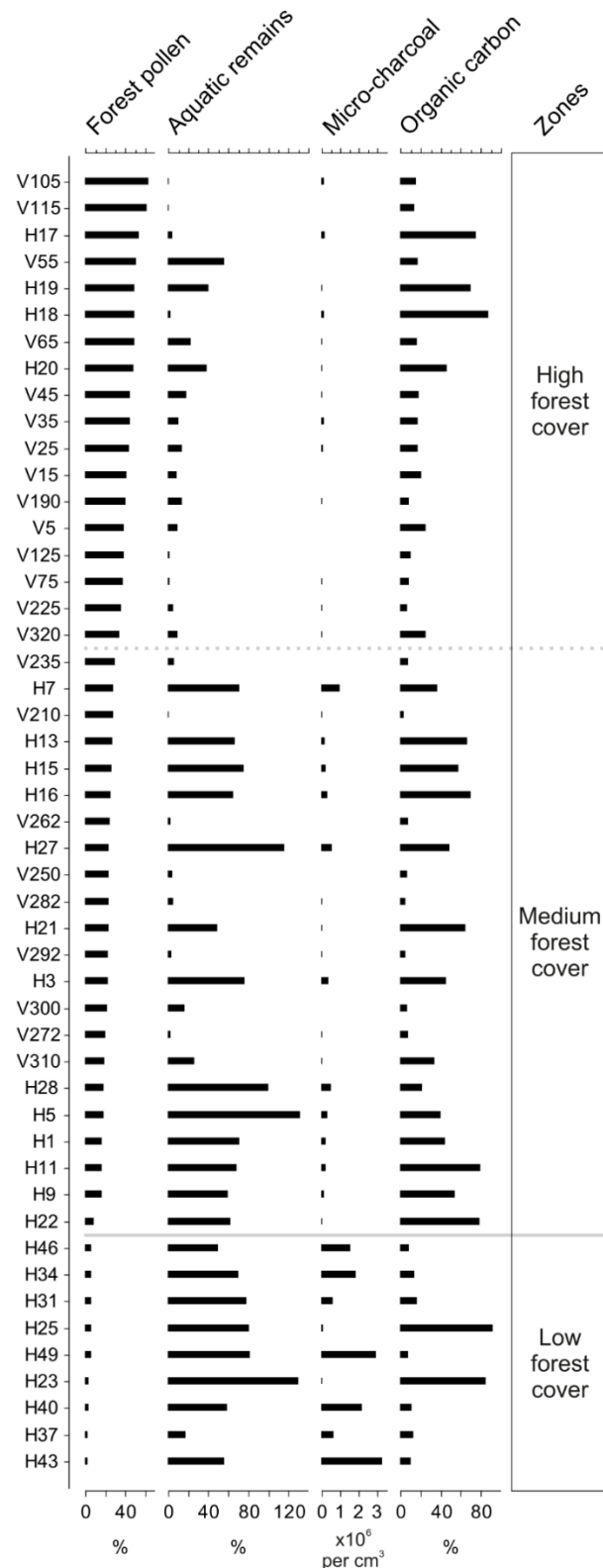


Figure 3.2 Palaeoenvironmental proxies from which environmental variables have been inferred. Samples are ordered based on increasing percentage of forest pollen. Forest pollen is based on the combined percentage of *Alnus*, *Weinmannia*, *Hedyosmum* and *Melastomataceae* in the sample relative to the total terrestrial pollen sum. Aquatics remains relate to the percentage abundance of total aquatic remains relative to the terrestrial pollen sum. Micro-charcoal plotted as fragments per cm³ of sediment. Organic carbon refers to the percent organic carbon loss during loss-on-ignition at 550 °C.

The presence of micro-charcoal on the palynomorph slides was used to identify periods of regional fire activity (Whitlock & Larsen, 2001). Samples were examined for microscopic charcoal fragments (5 μm -100 μm) and the exotic marker using a microscope at 200 x magnification. Counts were then expressed as the concentration of charcoal particles per cm^3 (Whitlock & Larsen, 2001).

Sediment samples of ca. 2 cm^3 were taken and processed for loss-on-ignition (LOI) analysis at depths corresponding to the palynomorph and charcoal samples. Sediment was dried at 40 °C for up to five days to remove moisture, followed by a controlled burn at 550 °C for four hours to remove organic carbon (Heiri et al., 2001). Weight loss was then converted to a percentage of the dry weight to determine the proportion of organic carbon within the sediment.

3.6.3 Zonation

Samples were first ordered sequentially based on the percentage of forest pollen representatives from the sample, i.e. along an environmental gradient of forest cover. Zonation was based upon NPP percentage abundance data of all morphotypes that occur in > 1 sample and with an abundance of > 2 % in at least one sample. Zones were then established using “optimal splitting by information content” (OSIC) using the program Psimpoll (Bennett, 2008), and the statistical significance of zones was tested using the broken stick method (Bennett, 1996). All data were plotted using the programme C2 (Juggins, 2007).

3.6.4 Data analysis

Canonical correspondence analysis (CCA) (ter Braak, 1986) was performed to investigate the influence of forest cover, available moisture, regional fire regime, and sediment composition on the distribution of fungal NPPs. A unimodal response model was used as the standard deviation was >2 and a constrained ordination was chosen as it is capable of visualising the relationship between taxa (fungal NPP data) and the potential environmental

mechanisms. CCA analysis was performed on NPP percentage data after a square-root transformation had been applied. The purpose of the square-root transformation was to stabilise variance within the assemblages and compensate for the occurrence of over-represented taxa that can occur with proxies that have a low dispersal potential, such as NPPs (Wilmshurst & McGlone, 2005). Within the CCA fungal NPP data were plotted against untransformed environmental data from forest pollen, aquatic remains, micro-charcoal, and organic carbon. Analysis of variance (ANOVA) was used to test the significance of the variation in fungal NPPs explained by the environmental variables. CCA was performed in R (R Core Team, 2015) using the package Vegan (Oksanen et al., 2016).

3.7 Results

3.7.1 Fungal non-pollen palynomorphs

A total of 52 samples was analysed, but three samples were determined to be barren of fungal NPPs (concentration < 2000 spores per cm³ in samples V90, V135 and V160) and were consequently excluded from subsequent analysis. Analysis of fungal NPPs within the remaining 49 samples identified 54 distinct fungal morphological types of which 51 met the requirements of the persistence (> 1 sample) and presence (> 2 % abundance in one sample) filters. Twenty-nine morphotypes were assigned to previously described types and are recorded in 'Appendix A' along with pertinent ecological information. Twenty-five previously undescribed morphotypes were recorded, photographed and described in 'Appendix B'.

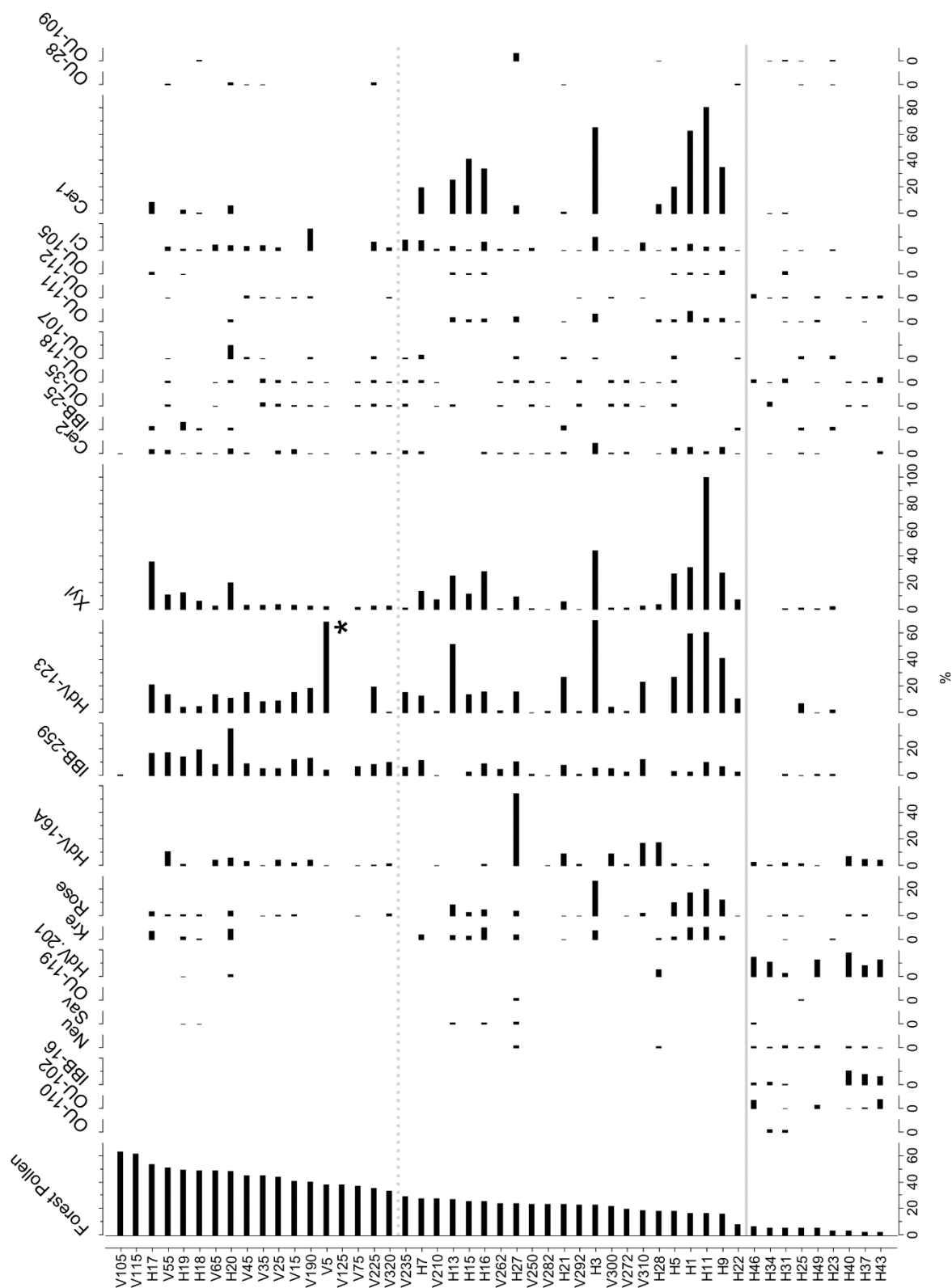
OSIC analysis of fungal NPP percentage data established three distinct zones which have been described based on their position along the forest cover environmental gradient: (i) low forest cover (< 8 % forest pollen relative to terrestrial pollen sum), (ii) medium forest cover (8-32 % forest pollen), and (iii) high forest cover (> 32 % forest pollen); the boundary between the low forest cover and medium forest cover zone was found to be statistically significant based on the broken stick method (Fig. 3.3).

Table 3.2 Abbreviations of taxa used in NPP diagram (Fig. 3.3) and CCA diagram (Fig. 3.4).

Identification	Morphotype	Abbreviation	Identification	Morphotype	Abbreviation
<i>Amphirosellinia</i> -type	Various	Amp	N/A	HdV-16A	HdV-16A
<i>Anthostomella fuegiana</i>	HdV-4	Anth	N/A	HdV-123	HdV-123
<i>Cercophora</i> -type 1	HdV-112	Cer1	N/A	HdV-201	HdV-201
<i>Cercophora</i> -type 2	HdV-1013	Cer2	N/A	HdV-495	HdV-495
Conidiophores	HdV-96	Con	N/A	HdV-733	HdV-733
<i>Coniochaeta</i> cf. <i>lignaria</i>	HdV-172	Cl	N/A	HdV-1058	HdV-1058
<i>Gaeumannomyces</i> or <i>Clasterosporium caricinum</i>	HdV-126	Gae	N/A	TM-211	TM-211
<i>Glomus</i>	HdV-207	Glo	N/A	UG-1194	UG-1194
<i>Kretzschmaria deusta</i>	HdV-44	Kre	N/A	IBB-16	IBB-16
<i>Neurospora</i> spp.	HdV-1093; 1351	Neu	N/A	IBB-25	IBB-25
<i>Podospora</i> -type	HdV-368	Pod	N/A	IBB-259	IBB-259
<i>Rosellinia</i> -type	HdV-1058	Rose	N/A	IBB-262	IBB-262
<i>Savoryella curvispora</i> -type	HdV-715	Sav			
<i>Sporormiella</i> -type	HdV-113	Spr			
<i>Sordaria</i> -type	HdV-55	Sor			
Sordariales	Various	Sord			
Xylariaceae-type	Various	Xyl			

3.7.1.1 Low forest cover zone (9 samples)

Within the low forest cover zone fungal NPP concentrations are low with only two samples above 10,000 spores per cm³ (H23 and H25). Samples are characterized by relatively high abundances of HdV-201 (0-18.6 %), IBB-16 (0-8.2 %), HdV-16A (0-5.5 %), OU-102 (0-7.5 %), and *Neurospora* (0-2.2 %). It is worth noting that morphotype OU-102 only occurs within the low forest cover zone and is present in six of the nine samples.



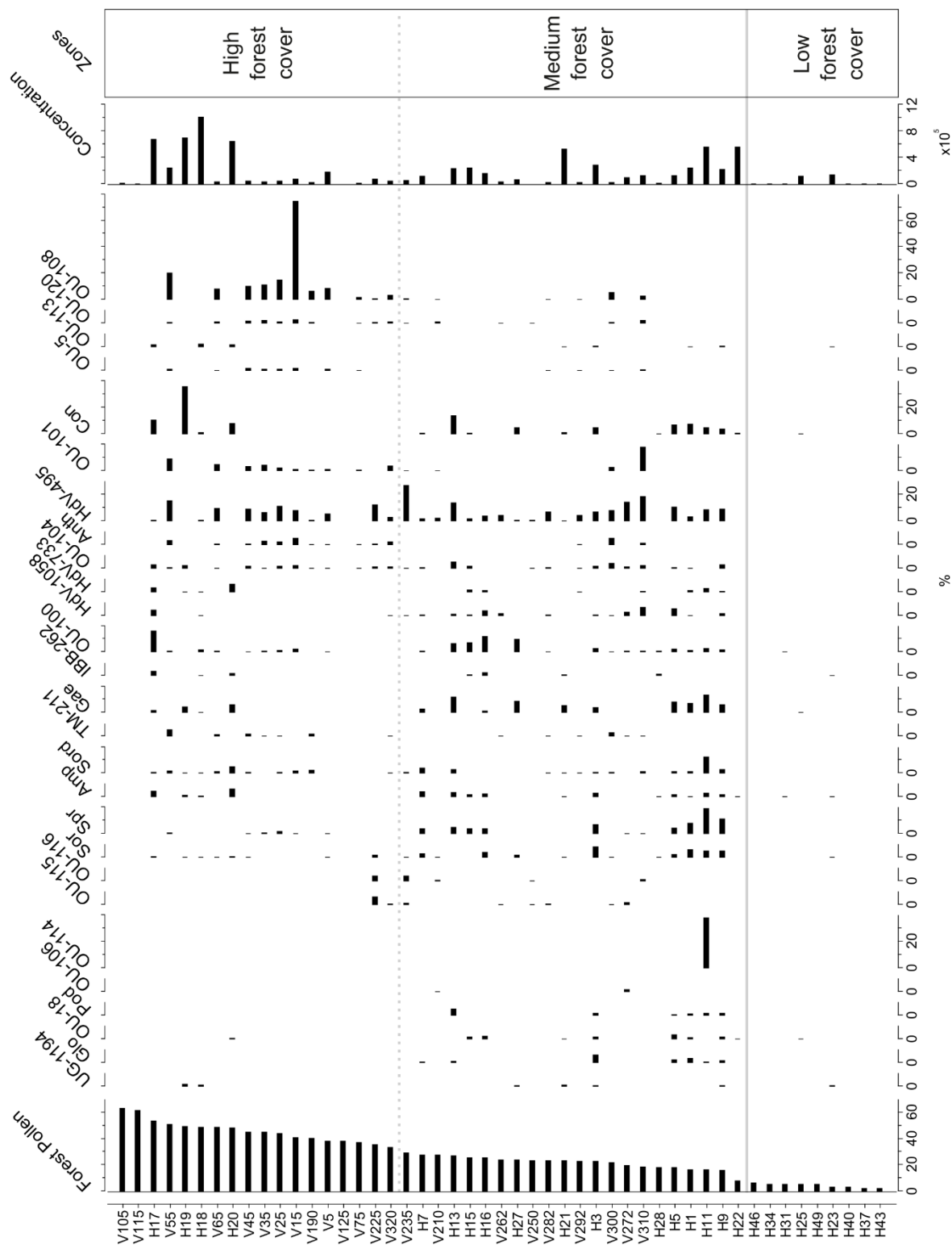


Figure 3.3 (*previous pages*) Fungal NPP assemblage data for all taxa occurring at > 2 % abundance in > 1 sample. Fungal NPP percentages are calculated relative to the total terrestrial pollen sum. Samples are ordered based on an increasing percentage of forest pollen.

3.7.1.2 Medium forest cover zone (22 samples)

Within the medium forest cover zone NPP concentrations fluctuate (ca. 3,400-570,000 spores per cm³; mean 180,000 spores per cm³); although it is worth noting that only three of the 22 samples (H11, H21 and H22) have high concentrations (> 500,000 per cm³). Samples are characterised by high abundances of Xylariaceae (0.3-100.6 %), *Cercophora*-type 1 (0-80.1 %), HdV-123 (0-698.3 %), HdV-495 (0-19.0 %), HdV-16A (0-54.6 %), and IBB-259 (0-12.9 %). It is also worth noting that OU-100 (0-12.4 %), and OU-104 (0-4.3 %) are most abundant within the medium forest zone.

3.7.1.3 High forest cover (18 samples)

Within the high forest cover zone fungal NPP concentrations range from ca. 10,000 to 1,000,000 spores per cm³. The most persistent and abundant fungal types include HdV-123 (0-68.7 %), Xylariaceae (0.1-20.7 %), HdV-495 (0-11.4 %), and IBB-259 (0.2-36.3 %). It is also worth noting that OU-108 (0-75.3 %) is more abundant in the high forest cover zone than any other zone, and that it reaches exceptionally high abundances in one sample (V25).

3.7.2 Environmental variables

The four independent indicators of environmental gradients (forest pollen, aquatic remains, micro-charcoal, and organic carbon) have been plotted against increasing forest pollen percentage data (Fig. 3.2). Forest pollen components (*Alnus*, *Hedyosmum*, *Weinmannia* and Melastomataceae) occur over a gradient of 2.5-63.5 % of the total terrestrial pollen sum. Aquatic remains in the low and medium forest cover zones fluctuate widely in abundance (low = 17-130 % of the total terrestrial pollen sum, mean 69 %; medium = 0.5-131 %, mean 49 %). While aquatic remains in the high forest pollen zone have less variance (0.8-56 %), and a lower mean (14.5 %). Micro-charcoal is most abundant within the zone of low forest cover where it occurs in concentrations of up to ca. 3,300,000 fragments per cm³ (sample H43). In the zones of medium and high forest cover micro-charcoal concentrations

progressively decrease (medium = < 1,000,000 fragments per cm³, high = < 200,000 fragments per cm³). The organic content of the sediment varies along the entire forest cover gradient with similar mean values (low = 29 %; medium = 36 %; high = 28 %) and a range of 3.2-92.0 % organic carbon.

3.7.3 Canonical correspondence analysis

CCA of the transformed fungal NPP data and the four environmental variables were plotted (Fig. 3.4). The explanatory (environmental) variables account for ca. 40 % (constrained inertia = 0.8187) of the variance in the fungal NPP percentage data (total inertia = 2.0438). The first two CCA axis accounting for 90 % of the explained variance (Eigenvalues CCA1 = 0.4235, CCA2 = 0.3198). The closest relationship of an environmental variable and a CCA axis is found between the aquatic remains and the positive side of Axis 2. The length attained by micro-charcoal points to a degree of affinity with the negative values of Axis 1. Forest pollen and organic carbon do not present a clear relationship with either of the axes based on the angles formed in the plot, but the direction of the trends suggest an inverse relationship between forest pollen and micro-charcoal (Fig. 3.4).

Fungal NPPs cluster into three broad groups. Morphotypes such as *Neurospora*, HdV-201 and IBB-16 co-vary with the micro-charcoal gradient. *Anthostomella fuegiana*, TM-211 and HdV-495 co-vary with the forest pollen gradient, and *Podospira*, *Gaeumannomyces* / *Clasteropsriom caricinum*, *Conidiophores* UG-1194 and IBB-25 co-vary with the aquatic remains and organic carbon gradients. Fungal NPPs that plot in the centre of the ordination are not strongly controlled by any one of the tested environmental variables (e.g. *Cercophora*-type 2 and HdV-1058), or are ubiquitous throughout the samples (e.g. *Xylariaceae*-type and HdV-16A).

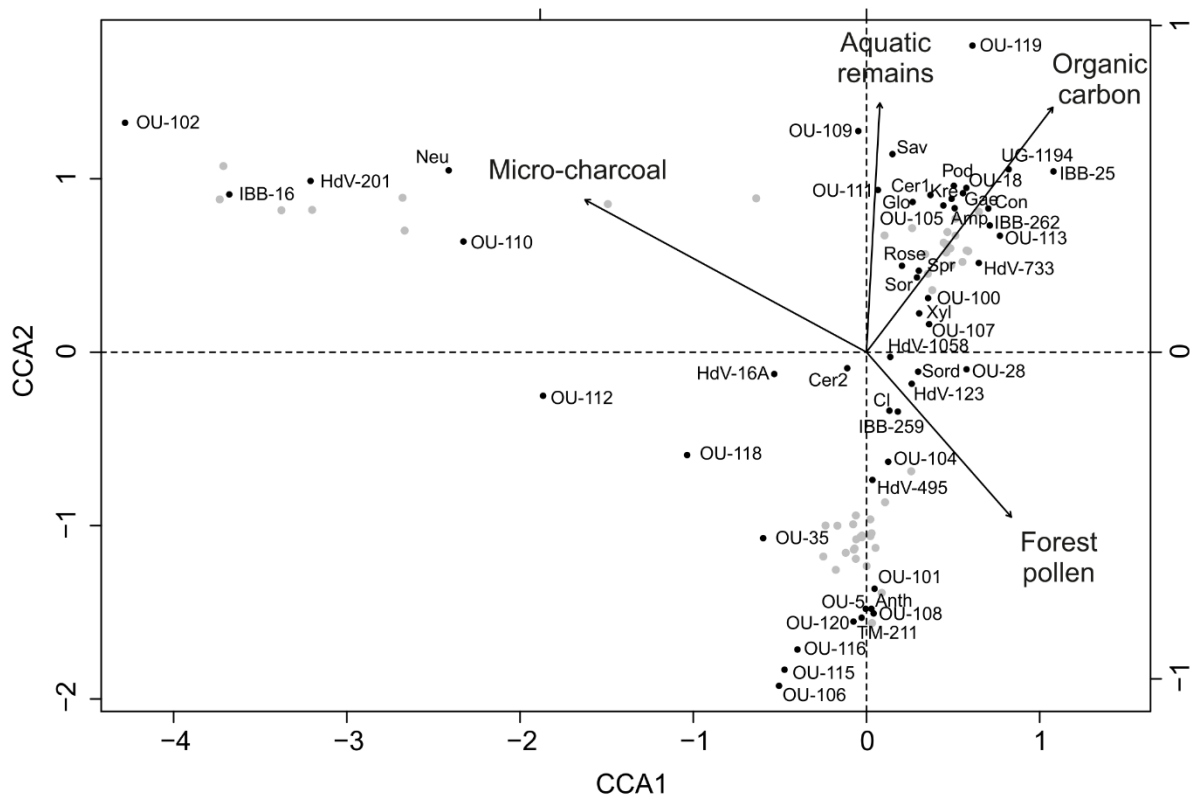


Figure 3.4 Canonical correspondence analysis (CCA) of NPP morphotypes and environmental variables. NPP morphotypes (black dots) and samples (grey dots) are plotted against palaeoenvironmental proxies of environmental variables (black arrows): forest pollen (forest cover), aquatic remains (available moisture), micro-charcoal (regional fire regime), and organic carbon (sediment composition).

3.8 Discussion

3.8.1 Variance in fungal NPPs along a gradient of forest cover in the Andes

NPPs show a statistically significant variation along the forest cover gradient sampled (2.5–63.5 %; Fig. 3.3). The occurrence of distinct NPP taxa assemblages in the three forest cover zones suggests that NPP assemblages could be used as indicators of forest cover on the eastern Andean flank.

The NPP assemblage in the low forest cover zone is characterised by an abundance of HdV-201, IBB-16, *Neurospora*, and HdV-16A. Interestingly, the two samples that do not contain the most abundant NPP taxa in the low forest cover zone (HdV-201) are also unusual in that they also have a sediment organic carbon ca. 60 % greater than any other sample (Fig. 3.2). The link between HdV-201 and organic carbon suggests that perhaps local factors which

limit organic input into the sediment are important for HdV-201. The presence of the carbonicolous fungal NPP *Neurospora* within the low forest cover zone in conjunction with high micro-charcoal indicate that regional and local fires likely occurred within areas of low forest cover. The high proportion of aquatic remains, here predominantly the semi-aquatic pollen Cyperaceae, might suggest a marsh type depositional environment. However, the low organic carbon content of the sediment indicates a low productivity environment.

Additional fungal NPPs from the low forest pollen zone include types indicative of more open environments (Fig. 3.3). HdV-201 occurs on helophytes in drying pools (van Geel et al., 1989) and IBB-16 within Páramo (high Andean grasslands) vegetation (Montoya et al., 2010). This combination of environmental conditions and fungal NPP morphotypes suggests an open depositional environment, with forest pollen input probably from extra-local sources. All samples from the low forest pollen zone belong to post-human arrival Huila sediments. The low abundance of forest pollen, low organic carbon content, and regional to local fire activity can be interpreted as indicative of landscapes degraded by humans based on comparisons with similar findings in modern studies of managed areas elsewhere in the Andes (Rull, 2006; Moscol-Olivera et al., 2009).

The statistically significant zonation at ca. 8 % forest cover occurs where the NPP assemblage changes to one containing an increase of morphotypes associated with decaying plant remains and high elevation grassland (Páramo) (Fig. 3.3). The zone of medium forest cover contains ligneous and saprophytic morphotypes such as *Cercophora*-type 1, Xylariaceae, *Rosellinia*-type, *Kretzschmaria deusta*, *Amphirosellinia* and *Coniochaeta* cf. *lingniaria* (van Geel et al., 2003; van Geel & Aptroot, 2006) indicative of an increase in woody taxa. Morphotypes HdV-123, HdV-495, HdV-733 and *Gaeumannomyces* / *Clasteropsprion caricinum* previously identified in marsh type environments are also abundant (van Geel, 1978; van Geel et al., 1981; Bakker & van Smeerdijk, 1982). The occurrence of these types in conjunction with the mycorrhizal fungi *Glomus*, an indicator of increased basin erosion and the coprophilous fungi *Sporormiella* and *Podospora*, suggests that the medium forest cover zone has been subjected to a degree of disturbance by herbivores and basin erosion. The transition from the medium to high forest cover zone is not statistically significant, however, some changes in the NPP assemblage can be observed. In the medium forest cover zone obligate coprophilous fungi (*Sporormiella* and *Podospora*)

and occasional coprophilous fungi (*Cercophora*-type 1 and *Sordaria*-type) are all at their most abundant along the forest gradient, suggesting a relationship between herbivores and medium forest cover. Furthermore, in the high forest cover zone *Anthostomella fuegiana*, an ascospore associated with the host plants Cyperaceae and Juncaceae (van Geel, 1978), and new morphotypes OU-5, OU-101, OU-108 and OU-120 are more prevalent than at any other point on the gradient. The reduction in micro-charcoal associated with the zone of high forest cover, the loss or reduction in the carbonicolous fungal spore *Neurospora*, disturbance indicator *Glomus*, and coprophilous fungi suggest an environment with little evidence of disturbance. Therefore, our data suggest that the fungal NPP assemblage formed by *Neurospora*, HdV-201, IBB-16, OU-102 and OU-110 could be tentatively used as a proxy for open environments (or degraded lands) within the montane forests of the eastern Andean flank.

3.8.2 Fungal NPP assemblages and environmental variables

The variables tested in this study form three groups of fungal NPPs along environmental gradients related to regional fire regime (micro-charcoal), depositional environment (organic carbon and aquatic remains), and forest cover (forest pollen) (Fig. 3.4). Together fire, depositional environment and forest cover explain ca. 40 % of the variance in the NPP dataset. Indicating that environmental variables not parameterised here (e.g. climate, human impact or disturbance, plant-fungal interactions) have a strong influence on assemblage composition.

3.8.2.1 Fire regime

Five NPP morphotypes have been identified as co-varying with regional fire regime (micro-charcoal) on the eastern Andean flank (upper left portion of Fig. 3.4); of these three have been previously described and two are newly described in this study. Three previously described morphotypes that co-vary with regional fire regime are: *Neurospora*, HdV-201 and IBB-16. *Neurospora* commonly occurs in the tropics on the surface of charred wood remains and is consequently seen as directly indicative of the presence of local fire events (Jacobson et al., 2006). In this study the strong affinity of *Neurospora* with fire regime supports the

interpretation of this NPP type with burning. The two other NPPs associated with fire in this study (HdV-201 and IBB-16) have been previously linked to helophyte remains in drier microhabitats (van Geel et al., 1989), and Páramo environments (Montoya et al., 2010) respectively. The association between the sole carbonicolous fungal NPP (*Neurospora*) and morphotypes indicative of a more open habitat (HdV-201 and IBB-16) fits with the inverse relationship between the fire regime and forest cover gradients in the CCA analysis (Fig. 3.4). The newly described morphotypes adjacent to the micro-charcoal gradient (OU-102 and OU-110) occur only within seven samples (H31 to H49), which contain seven of the eight highest concentrations of micro-charcoal in the whole dataset (Fig. 3.3). These seven samples also have low forest cover (< 8 %) and organic content (< 17 %). The fungal NPP assemblage of *Neurospora*, HdV-201, IBB-16, OU-102 and OU-110 is therefore suggested to be broadly indicative of elevated fire regimes and appear in semi-open environments, with poor or degraded soils.

3.8.2.2 Depositional environment

Aquatic remains (moisture availability) and organic carbon (sediment composition) co-vary with the greatest abundance of NPP morphotypes (upper right region of the ordination in Fig. 3.4). The taxa comprise a number of fungal NPP morphotypes with a variety of autoecological characteristics suggested to relate to the dynamic and heterogeneous nature of eastern Andean montane landscape. Morphotypes IBB-262 and IBB-25 have previously been identified from within the cloud forest and Páramo environments of Colombia and Venezuela (Hooghiemstra, 1984; Montoya et al., 2010). *Amphirosellinia* sp. and *Kretzschmaria deusta* are parasitic tree fungi often associated with rotting wood (Ju et al., 2004; Innes et al., 2010). *Kretzschmaria deusta* occurs on common Andean montane forest taxa such as *Alnus* sp. and *Ilex* sp. (van Geel & Andersen, 1988), and increased abundance has been related to severe rainstorms during the Holocene (van Geel et al., 2013). While morphotype HdV-733 and *Savoryella curvispora* occur in mesotrophic marshes dominated by wetland grasses (Bakker & van Smeerdijk, 1982), of which *Gaeumannomyces* sp. / *Clasteropsprion caricinum* are the hyphopodium of leaf parasites on Cyperaceae. The coprophilous fungi *Podospora* and *Sporormiella* also occur along the organic carbon gradient suggesting a possible link between the presence of herbivores and increased organic

carbon. The newly described morphotypes (OU-18, OU-105, OU-113 and OU-119) that occur in this region of the CCA are from samples which exhibit high organic content (41-75 %), but variable forest cover (3-54 %). Fungal NPP assemblages containing *Cercophora*-type 1, *Amphirosellinia* sp., *Kretzschmaria deusta*, *Gaeumannomyces* sp./ *Clasteropsprion caricinum*, IBB-262, IBB-25, UG-1194, OU-18, OU-105, OU-113 and OU-119 are therefore suggested to be broadly indicative of organic rich depositional environments; however, it is likely that multiple different factors are responsible for the elevated organic levels, e.g. elevate sediment organic carbon content could result from high forest cover and/or presence of herbivores.

3.8.2.3 Forest cover

The forest pollen gradient covaries closely with two previously identified NPP morphotypes (lower right region Fig. 3.4). HdV-495 has been identified within the Andean montane forest and Páramo of Venezuela (Montoya et al., 2010), and IBB-259 from within montane settings in Europe (López-Vila et al., 2014). The lack of NPP morphotypes closely associated with the forest pollen gradient indicates a weak relationship between forest cover and fungal NPP assemblage. The absence of a close relationship between forest cover and the overall NPP assemblage supports the findings of previous studies that NPPs provide a local signal (Wilmshurst & McGlone, 2005; Montoya et al., 2010).

It is interesting to note that the samples most closely aligned with high forest cover are from the pre-human Vinillos sediments and are associated primarily with new morphotypes OU-5, OU-101, OU-106, OU-108, OU-115, OU-116 and OU-120 (lower central region Fig. 3.4). However, the lack of a clear association with our environmental variables suggests that unparameterised factors are primarily driving fungal NPP assemblages in the pre-human Andean landscape. Based on the data available it could be suggested that the inverse relationship of these morphotypes with the gradients for aquatic remains and organic carbon may indicate that this unidentified gradient corresponds to other edaphic factors. The absence of NPP identifications and environmental association along the forest cover gradient illustrates that much research is still required in this area, but suggests that further ecological information will be gleaned about pre-human Andean landscapes as the NPP record becomes better understood.

3.9 Conclusions

Here I present 54 distinct fungal NPP types identified from Quaternary sedimentary archives from the eastern Andean flank of Ecuador. This work represents the first record of fungal NPPs from Ecuador and identifies 25 new fungal NPP morphotypes (Appendix B and Fig. 8.1). Along an environmental gradient of forest cover fungal NPPs show a statistically significant change between low and medium levels of forest cover. The NPP assemblage found in low forest cover is characterised by the morphotypes *Neurospora*, HdV-201, IBB-16, OU-102 and OU-110. Increases in forest cover above this point produce no statistically significant change in NPP assemblage composition. However, preliminary groups of morphotypes more common in medium and high forest cover include *Cercophora*-type 1, Xylariaceae, *Rosellinia*-type, *Kretzschmaria deusta*, *Glomus*, *Podospora*, *Sporormiella*, HdV-16A, OU-18 and *Anthostomella fuegiana*, OU-5, OU-101, OU-108, OU-120 respectively.

The comparison of fungal NPPs assemblage data with independent environmental proxy data derived from sedimentary archives within a CCA has demonstrated that this method can be used to improve our understanding of NPP autoecology. This improved understanding of NPPs will, I hope, improve palaeoenvironmental reconstructions from the Andes. However, future work undertaking modern NPP altitudinal transects in conjunction with mycological field studies to understand plant-fungal interactions in these biodiverse forests are required in order to capitalise on the use of NPPs as an effective palaeoecological proxy in the Neotropics. Amongst the environmental variables considered fire regime (micro-charcoal) and depositional environment (aquatic remains and organic carbon) were found to be the most important explanatory variables. Moreover, the importance of fire occurrence has been related to the only statistically significant zone (< 8 % forest cover) found, which is characterised by the fungal NPP assemblage *Neurospora*, HdV-201, IBB-16, OU-102 and OU-110, representing an open and degraded landscape within the montane forests of the eastern Andean flank that only occurs subsequent to human arrival on the continent. Further studies of modern and sedimentary samples along a variety of environmental gradients are required to improve the utility of fungal NPPs as a proxy within the Andes. To progress understanding of NPPs in the Andes I recommend that all NPP remains should be recorded as part of any palynological investigation, even when the identities of the NPP morphotypes are unknown.

3.10 Author contributions and acknowledgments

This chapter was written by Nicholas Loughlin (N.J.D.L.) with input and support of the supervisory team. N.J.D.L. prepared the samples, collected and analysed the data, wrote the chapter and created the figures. N.J.D.L., Encarni Montoya and William Gosling collected the Huila samples. Radiocarbon dating was undertaken by Pauline Gulliver at the NERC Radiocarbon Facility East Kilbride (NRCF010001). Annemarie Philips (University of Amsterdam, Netherlands) provided assistance with sample preparation. Patricia Mothes (Instituto Geofísico, Escuela Politécnica Nacional, Ecuador) located the Vinillos and Huila sites. Encarni Montoya and William Gosling along with Hayley Keen, Frazer Matthews-Bird and James Malley (all The Open University, UK) collected the Vinillos samples. As part of the submission of this chapter to the journal *Quaternary Research* Bas van Geel (University of Amsterdam, Netherlands), an anonymous reviewer and the guest journal editor Mark Bush (University of Florida, USA) commented on the manuscript and provided constructive feedback which has been incorporated into this chapter.

Chapter 4

4 Landscape-scale drivers of glacial ecosystem change in the montane forests of the eastern Andean flank

4.1 Overview

In this chapter a multiproxy palaeoecological analysis of a pre-human arrival montane forest environment is undertaken to detail the landscape-scale processes driving ecosystem change. This chapter is based on a manuscript published in the journal *Palaeogeography, Palaeoclimatology, Palaeoecology*.

Loughlin, N.J.D., Gosling, W.D., Coe, A.L., Guliver, P., Mothes, P. Montoya, E. (2018) Landscape-scale drivers of glacial ecosystem change in the montane forests of the eastern Andean flank. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 489(1): 198-208.

4.2 Abstract

Understanding the impact of landscape-scale disturbance events during the last glacial period is vital in accurately reconstructing the ecosystem dynamics of montane environments. Here, a sedimentary succession from in the tropical montane cloud forest of the eastern Andean flank of Ecuador provides evidence of the role of non-climate drivers of vegetation change (volcanic events, fire regime and herbivory) during the late-Pleistocene. Multiproxy analysis (pollen, non-pollen palynomorphs, charcoal, geochemistry and carbon content) of the sediments, radiocarbon dated to ca. 45-42 ka, provide a snap shot of the depositional environment, vegetation community and non-climate drivers of ecosystem dynamics. The geomorphology of the Vinillos study area, along with the organic-carbon content, and aquatic remains suggest deposition took place near a valley floor in a swamp or shallow water environment. The pollen assemblage initially composed primarily of herbaceous types (Poaceae-Asteraceae-Solanaceae) is replaced by assemblages characterised by Andean forest taxa, (first Melastomataceae-*Weinmannia-Ilex*, and later, *Alnus-Hedyosmum-Myrica*). The pollen assemblages have no modern analogues in the tropical montane cloud forest of Ecuador. High micro-charcoal and rare macro-charcoal abundances co-occur with volcanic tephra deposits suggesting transportation from extra-local regions and that volcanic eruptions were an important source of ignition in the wider glacial landscape. The presence of the coprophilous fungi *Sporormiella* reveals the occurrence of herbivores in the glacial montane forest landscape. Pollen analysis indicates a stable regional vegetation community, with changes in vegetation population co-varying with large volcanic tephra deposits suggesting that the structure of the glacial vegetation community at Vinillos was driven by volcanic activity.

4.3 Introduction

Mid-elevation tropical forests have been identified as some of the most biodiverse yet at risk terrestrial ecosystems in the world due to their high degree of endemism, sensitivity to climate change and anthropogenic impact (Churchill et al., 1995; Hamilton et al., 1995; Bruijnzeel et al., 2011). However, questions remain regarding their ecosystem processes and the role of environmental drivers as mechanisms of ecosystem change.

Tropical montane cloud forests (TMCF) are distinguished from other types of tropical forest by their association with montane environments immersed in frequent ground level cloud (Grubb, 1971, 1977). TMCF on the eastern Andean flank of northern Ecuador occur between ca. 1200-3600 metres above sea level (m asl) and inhabit a dynamic and heterogeneous landscape (Harling, 1979; Sierra, 1999). Steep topographical changes produce environmental gradients that change abruptly with variation in precipitation, temperature and solar radiation (Sarmiento, 1986). Changes in climate associated with cloud cover play an important role in natural cloud forest structure and composition (Churchill et al., 1995; Hamilton et al., 1995; Fahey et al., 2016). However, modern anthropogenic pressures (e.g. land-use change, land-cover modification, pollution) arguably exceeded climate as the dominant control on vegetation structure through much of the TMCF of the eastern Andean flank (Sarmiento, 1995).

Non-climate drivers of ecosystem change in TMCF play a key role in increasing landscape and vegetation heterogeneity (Crausbay & Martin, 2016). Modern natural (non-human) drivers of ecosystem change include abiotic processes such as volcanic eruptions, earthquakes, landslides and fire, while biotic processes such as plant-animal interactions, disease, forest die-back and a variety of edaphic factors, e.g. nutrient limitation are all associated with landscape-scale modification of the environment. The stochastic nature of these abiotic and biotic drivers, coupled with high landscape heterogeneity can alter vegetation at a local to regional scale, over geologically short periods of time. In order to better understand ecosystem function in montane environments the role of non-climate drivers of vegetation change during different climate regimes (e.g. glacial periods), and in the absence of modern anthropogenic impact, needs to be ascertained.

Long sedimentary records from large lakes indicate climate is the primary driver of vegetation change over millennial scale time frames within the Andes (van der Hammen & Hooghiemstra, 2003; Hanselman et al., 2011). The only lake records from within the TMCF habitat of the eastern Andean flank that extend from prior to the last glacial maximum occur at Lake Consuelo in southern Peru (Bush et al., 2004b; Urrego et al., 2005, 2010) and at Funza and Fúquene in central Colombia (Hooghiemstra, 1984; van der Hammen & Hooghiemstra, 2003; Bogotá-A et al., 2011). Analysis of past vegetation change in the TMCF of the eastern Andean flank of Ecuador is limited due to the paucity of suitably preserved

sediments. Palynological analysis of discontinuous sediments from cliff sections at the Mera, Erazo and San Juan de Bosco sites indicate changing forest assemblages through the Quaternary are driven by long-term changes in climate (Liu & Colinvaux, 1985; Bush et al., 1990; Colinvaux et al., 1997; Cárdenas et al., 2011, 2014; Keen, 2015). However, the role of short-term non-climate drivers of vegetation change has yet to be investigated in this setting.

Here I use a multi-proxy approach (pollen, non-pollen palynomorphs, wood macro-remains, charcoal, geochemistry and carbon content) to reconstruct a snap shot of a glacial montane forest vegetation community. I assess the role of volcanic activity (volcanic tephra layers), fire regime (charcoal) and herbivory (*Sporormiella*) as ecosystem drivers of vegetation change in a glacial montane forest and discuss the importance of incorporating non-climate drivers of vegetation change into palaeoecological reconstructions of TMCF.

4.4 Study site

A new section was located at Vinillos (00° 36.047' S, 77° 50.814' W), near the town of Cosanga in the Napo Province, Ecuador. The Vinillos site is situated at 2090 m asl between the Cordillera Real and Napo Uplift on the eastern Andean flank of northern Ecuador (Fig. 4.1). The exposure is located on the eastern side of the Cosanga Valley, and was uncovered during construction of the Troncal Amazónica (E45); the highway adjacent to the Río Cosanga.

Modern climate data from the study region is sparse, however, 15 years of data from the nearby town of Baeza (Fig. 4.1) indicates an average of 2320 mm of precipitation per annum (Valencia et al., 1999). High levels of orographic rainfall and semi-permanent ground level cloud lead to persistent moist conditions (Harling, 1979). Mean annual temperatures range from 16-20 °C throughout the year due to stable levels of solar radiation and low seasonality (Harling, 1979; Galeas & Guevara, 2012), however, diurnal changes in temperature of up to 20 °C can occur at higher elevations, acting as a much more significant control on vegetation distribution than seasonal changes in temperature (Neill & Jørgensen, 1999).

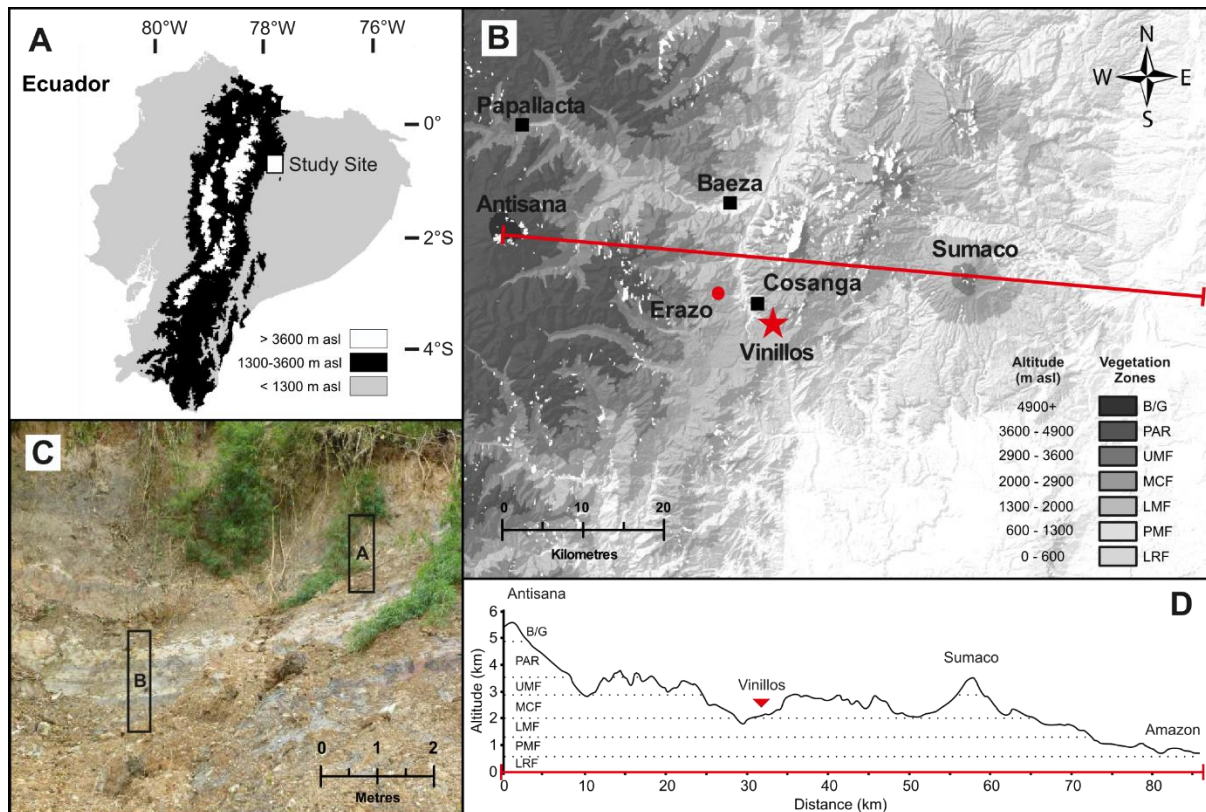


Figure 4.1 Study sites. **A.** Location of study site in Ecuador, within montane forest vegetation zone (1300-3600 m asl), **B.** Topographic map of study region with generalised vegetation zone from Sierra (1999). LRF-lowland rainforest; PMF – pre-montane forest; LMF-lower montane forest; MCF-montane cloud forest; UMF-upper montane forest; PAR-páramo; B/G-barren / glaciers. Black squares indicate towns, red circle is Erazo section (Cárdenas et al., 2011), and red star is the location of the Vinillos exposure. Red line represents cross-section as seen in 'D', **C.** Photograph of Vinillos exposure prior to sampling and position of Section A and B, **D.** Cross-section of eastern Andean flank through Antisana and Sumaco volcanos, with generalized vegetation zones and position of Vinillos.

Today the Vinillos section is situated within tropical montane cloud forest vegetation (Fig. 4.1) (Webster, 1995; Neill, 1999b; Sierra, 1999). The modern vegetation at Vinillos is composed primarily of Andean forest elements such as *Arecaceae*, *Betulaceae* (*Alnus*), *Chloranthaceae* (*Hedyosmum*), *Cunoniaceae* (*Weinmannia*), *Ericaceae*, *Fabaceae*, *Lauraceae*, *Melastomataceae*, *Moraceae*, *Rubiaceae* and *Urticaceae* (*Cecropia*) with abundant epiphytic mosses, lichens, ferns, *Bromeliaceae*, *Araceae* and *Orchidaceae* (Grubb et al., 1963; Valencia et al., 1998; Cárdenas et al., 2014).

Anthropogenic disturbance and deforestation in the region means that the modern vegetation is a mosaic of arable land, pastures and secondary forest. Modern pollen-vegetation relationships have not been studied extensively in the region of Vinillos, however, a modern pollen altitudinal transect (1895m-2220 m asl) from the nearby Erazo

site (Fig. 4.1) does provide a representation of the human impacted pollen signal showing an over representation of the disturbance indicator *Cecropia* (Cárdenas et al., 2014). Studies of pollen-vegetation relationships from montane forests elsewhere in the Andes indicate that the modern pollen rain of tropical montane cloud forests is comprised of a combination of Andean and lowland forest taxa (Weng et al., 2004b; Rull, 2006).

4.5 Methods

4.5.1 Sediment sampling

The Vinillos section is composed of 325 cm of interbedded organic layers (identified with the prefix O) and volcanic tephra deposits (identified with the prefix T) (Fig. 4.2). Forty-four sediment samples were collected in 2012 through the six organic layers at approximately 5 cm intervals. A further four samples were collected, one from each of the four volcanic tephra layers. The exposure was cleared of surface sediment and vegetation prior to sampling, which commenced in the uppermost dark-brown organic layer below the weathered surface soils. A knife was used to extract 1 cm wedges of sediment from the section, which were placed in zip locked bags, labelled and kept cool prior to transport to The Open University (UK) where they were stored in a cold store (3-5 °C). Descriptions of the sediments were recorded during sampling.

4.5.2 Radiocarbon dating

Accelerator mass spectrometry (AMS) radiocarbon (^{14}C) dating of two palynomorph residues from the top and base of the Vinillos section was undertaken to constrain the age of the sediments (Table 4.1). Palynomorph residues were used as they have been shown to produce more reliable ages than bulk samples in regions of high rainfall (Vandergoes & Prior, 2003; Newnham et al., 2007). Guidelines, based on standard palynological protocols (Faegri & Iversen, 1989) were provided by the Natural Environment Research Council (NERC) Radiocarbon Facility-East Kilbride (NRCF). Preparation included the mechanical sieving of the sediment at 100 μm and the use of HCL, KOH and HF to concentrate palynomorphs from the bulk sediment.

4.5.3 Loss-on-ignition

Forty-eight 2 cm³ subsamples of sediment were extracted for loss-on-ignition (LOI) analysis. A standard LOI protocol was undertaken (Heiri et al., 2001). Samples were dried at 40 °C for up to 5 days to remove moisture, followed by controlled burns at 550 °C for 4 hours to remove organics, and 950 °C for 2 hours to remove carbonates, with the remaining material classified as siliciclastics. Weighing of samples took place after each phase and the weight loss converted to a percentage of the dry weight.

4.5.4 X-ray fluorescence

Major element analysis using X-ray fluorescence (XRF) was undertaken on the four tephra layers and two internal standards using standard protocols (Thomas & Haukka, 1978; Enzweiler & Webb, 1996). Glass disks were produced and analysed using an ARL 8420+ dual goniometer wavelength dispersive XRF spectrometer at The Open University to determine the major element composition (SiO₂, TiO₂, Al₂O₃, Fe₂O₃, MnO, MgO, CaO, Na₂O, K₂O, P₂O₅) of the tephra material.

4.5.5 Charcoal analysis

Twenty-nine samples from the organic sediments were examined for microscopic charcoal (5-100 µm) in the slides mounted for palynomorphs analysis. Fifty random fields of view from each palynomorph slide were recorded for microscopic charcoal remains and exotic *Lycopodium* at 200x magnification (Clark & Patterson, 1997; Whitlock & Larsen, 2001). Micro-charcoal values were then converted to concentration per cm³. Fifty 1 cm³ subsamples of material were also processed and analysed for macroscopic charcoal particles (> 100 µm). Sediment was deflocculated in 15 ml of a 10 % solution of KOH at 80 °C for 20 minutes and then washed through a sieve at 100 µm (Whitlock & Larsen, 2001). The remaining residue was then analysed under a low power (20x) microscope in a bogorov tray and all charcoal particles recorded. Particles were identified by their angular form, brittle nature and high reflectivity (Clark & Royall, 1995).

4.5.6 Palynomorph analysis

Twenty-six discrete sediment samples were chosen for the examination of palynomorphs at approximately 10 cm intervals through the organic layers and in all of the volcanic tephra layers. Organic samples of 1 cm³ were processed using standard laboratory procedures (Faegri & Iversen, 1989). Volcanic tephra samples of 6 cm³ were processed using density separation (Bromoform; 2 mol), due to the highly siliciclastic nature of the sediments and low palynomorph concentration (Moore et al., 1991). Samples using these two methods of palynomorph recovery have been shown to be directly comparable (Campbell et al., 2016). The addition of an exotic marker; here *Lycopodium* batch #124961: averaging 12,542 ± 931 spores per tablet, was added in order to determine palynomorph concentrations (Stockmarr, 1971). Samples were mounted in glycerol on glass slides and counted at 400x and 1000x magnification using a Nikon Eclipse 50i microscope. Counting of all palynomorphs (pollen, algae, fungal and zoological remains) was undertaken until a minimum of 300 terrestrial pollen grains (305-474) were recorded per sample, corresponding to between 0-113 algal remains, 0-2620 fungal NPPs and 0-12 zoological remains. Reference material at The Open University, an open access online pollen database (Bush & Weng, 2007) and published pollen atlases (Hooghiemstra, 1984; Roubik & Moreno, 1991; Colinvaux et al., 1999), were used to identify pollen grains. Non-pollen palynomorph (NPP) identification was undertaken using the available literature (van Geel, 1978; van Geel et al., 1981, 1983, 1989, 2003, 2011; Bakker & van Smeerdijk, 1982; Hooghiemstra, 1984; van Smeerdijk, 1989; Rull & Vegas-Vilarrúbia, 1998, 1999; van Geel & Aptroot, 2006; Rull et al., 2008; Cugny et al., 2010; Montoya et al., 2010, 2012; Gelorini et al., 2011; López-Vila et al., 2014). New NPP morphotypes (assigned with the prefix OU) were recorded and are described in Appendix B.

4.5.7 Zonation of palynomorphs

Statistically significant zones were established for pollen assemblages in the program PSIMPOLL (Bennett, 2008). Data were filtered to include only terrestrial pollen taxa that occurred in > 1 sample and at an abundance of > 2 % in at least a single sample. Aquatic elements, spores and NPPs were excluded. Zonation was performed by optimal splitting by information content, using the broken stick method to determine the significant number of

zones (Bennett, 1996). The pollen assemblages were then applied to the palynomorph diagrams which were plotted in the program C2 (Juggins, 2007).

4.6 Results

4.6.1 Chronology

Radiocarbon dating from the upper and lower portion of the Vinillos section (20 cm and 309 cm) returned dates whose one standard deviation error overlap. Calibration of reported dates was undertaken in OxCal 4.2.4 (Bronk Ramsey et al., 2013) using the IntCal13 atmospheric curve (Reimer et al., 2013). Uncertainties in the dates indicate it is not possible to construct a robust chronology or establish the rate of sedimentation. However, the radiocarbon dates do indicate deposition of the Vinillos sediments took place during the late Pleistocene ca. 45-42 ka (Table 4.1).

Table 4.1 Accelerator mass spectrometry (AMS) radiocarbon (^{14}C) dating of Vinillos palynomorph residues.

Publication Code	Sample Depth (cm)	$\delta^{13}\text{C}_{\text{VPDB}}^1$ (‰)	Radiocarbon Age ² (yr B.P. $\pm 1\sigma$)	Calibrated* Radiocarbon Age (yr B.P. $\pm 1\sigma$)	Calibrated* Radiocarbon Age (Median Probability)
SUERC-58952	20	-27.4	38,503 \pm 968	41,885-43,325	42,670
SUERC-58953	309	-27.1	40,524 \pm 1,245	43,091-45,218	44,300

¹ $\delta^{13}\text{C}_{\text{VPDB}}$ (‰) values were determined from using an aliquot of sample CO_2 and were measured on a dual inlet stable isotope mass spectrometer (Thermo Scientific Delta V Plus) and are representative of $\delta^{13}\text{C}$ in the pre-treated sample material.

² Conventional radiocarbon years B.P. (relative to AD 1950), expressed at the $\pm 1\sigma$ level for overall analytical confidence. Calculated from 14/13 ratios analysed by AMS which were subsequently corrected to $\delta^{13}\text{C}_{\text{VPDB}} = -25$ ‰ using the $\delta^{13}\text{C}$ values listed in Table 4.1 and corrected for background contamination using the NERC Quartz tube combustion background of $+0.17 \pm 0.1$ % modern carbon.

4.6.2 Sediments

The Vinillos section is composed of dark-brown to black organic layers with occasional pale grey lenses of volcanic ash interbedded with pale grey to beige volcanic tephra deposits. The sedimentary succession is composed of two offset portions, starting from the base of the exposure, Section B (SB) occurs from 325 cm to 140 cm and Section A (SA) from 135 cm to 0cm, separated by a 5 cm sand layer that was not sampled, giving an overall thickness of 325 cm in length (Fig. 4.2). LOI of the basal 20 cm of the Vinillos section (a black organic-rich clay) indicates an organic carbon content of 22-34 wt %. Organic carbon is reduced to 3-9 wt % for the remainder of SB following the first occurrences of lenses of volcanic ash occurring at ca. 300 cm. Units SAO2 and SAO1 which make up the organic units of SA show a gradual increase in organic carbon through the beds after each tephra layer from 9-16 wt % and 8-20 wt % respectively. Carbonate content is low throughout the Vinillos section ranging from 0.5-2.5 wt %, with a mean of 0.9 wt %. Two unidentified large (> 30 cm in length and > 10 cm in diameter) wood macro-fossils were recovered from the outcrop, one within organic bed SBO1 and the other in SBO2 where it meets tephra layer T4 (Fig. 4.4).

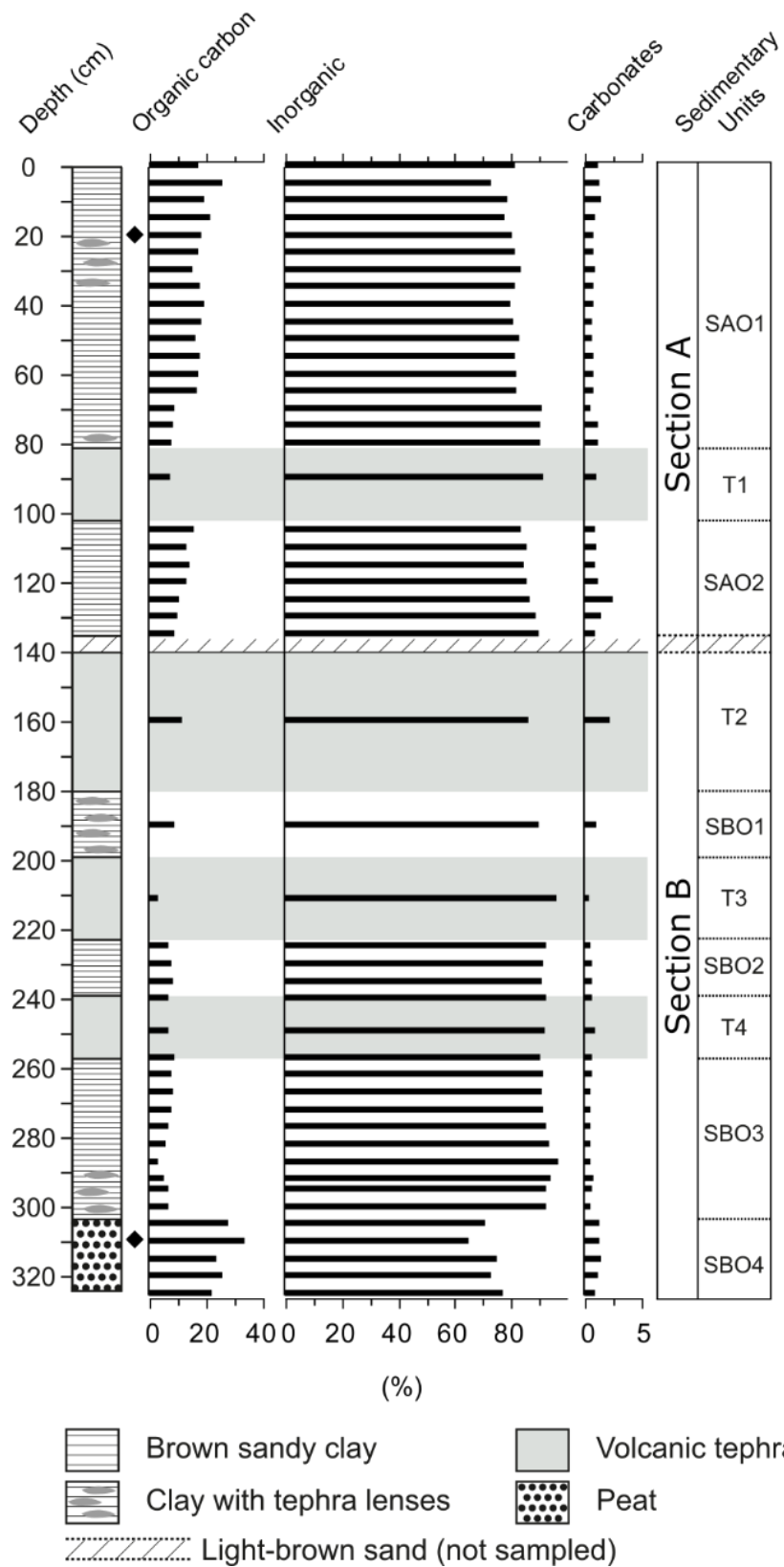


Figure 4.2 Sediment profile. Loss-on-ignition results of 48 samples indicating the percent weight loss of organic material, carbonate material and remaining inorganic material.

4.6.3 Volcanic tephra layers

Four discrete volcanic tephra layers of different thicknesses were identified at Vinillos, T1 (18 cm), T2 (25 cm), T3 (40 cm) and T4 (23 cm). Geochemical analysis of the volcanic tephra layers using XRF indicate chemical compositions that can be characterised as an andesite (T1), basaltic andesite (T2), trachy-andesite (T3) and dacite (T4) (Fig. 4.3). Combustion of samples using LOI prior to XRF indicate that volcanic tephra samples contain between 3-12 % organic carbon and are therefore not purely inorganic volcanic deposits (Fig. 4.2). Pollen was detected and identified within each tephra layer (Fig. 4.5). Fungal NPPs were identified within T3 and T4, but no discernible NPP remains were identified from T1 and T2 (Fig. 4.6).

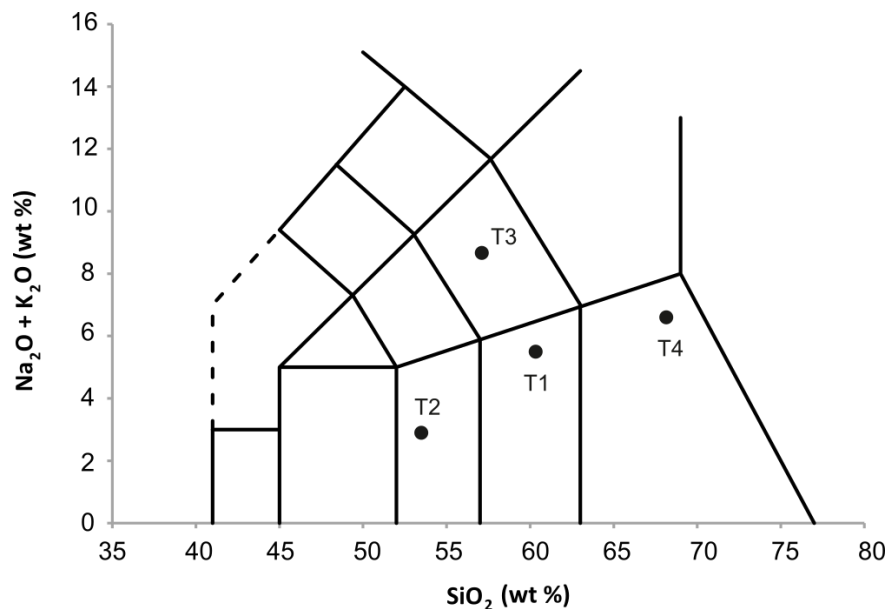


Figure 4.3 TAS diagram of X-ray fluorescence data on volcanic tephra layers. T1-andesite; T2-basaltic andesite; T3-trachy-andesite; T4-dacite.

4.6.4 Macro- and micro-charcoal

Macro-charcoal was recovered from eleven of the forty-eight samples examined. The charcoal occurred at a concentration of 1-26 fragments per cm^3 . Nine of the eleven samples which contained macro-charcoal occur in the volcanic tephra layers or directly adjacent to them, the two other samples were from near the base of SBO3, concomitant with the first organic sediments to contain volcanic ash lenses. Micro-charcoal is present in each of the 29 samples analysed. The abundance of micro-charcoal ranged from 2,500-140,000 fragments

per cm³, with a mean of 44,500 fragments per cm³. Maximum micro-charcoal concentrations correlate with the maximum macro-charcoal concentration, occurring directly below T1 and in the samples collected at a height of 35-25 cm (SAO1) where the youngest organic samples occur with volcanic ash lenses.

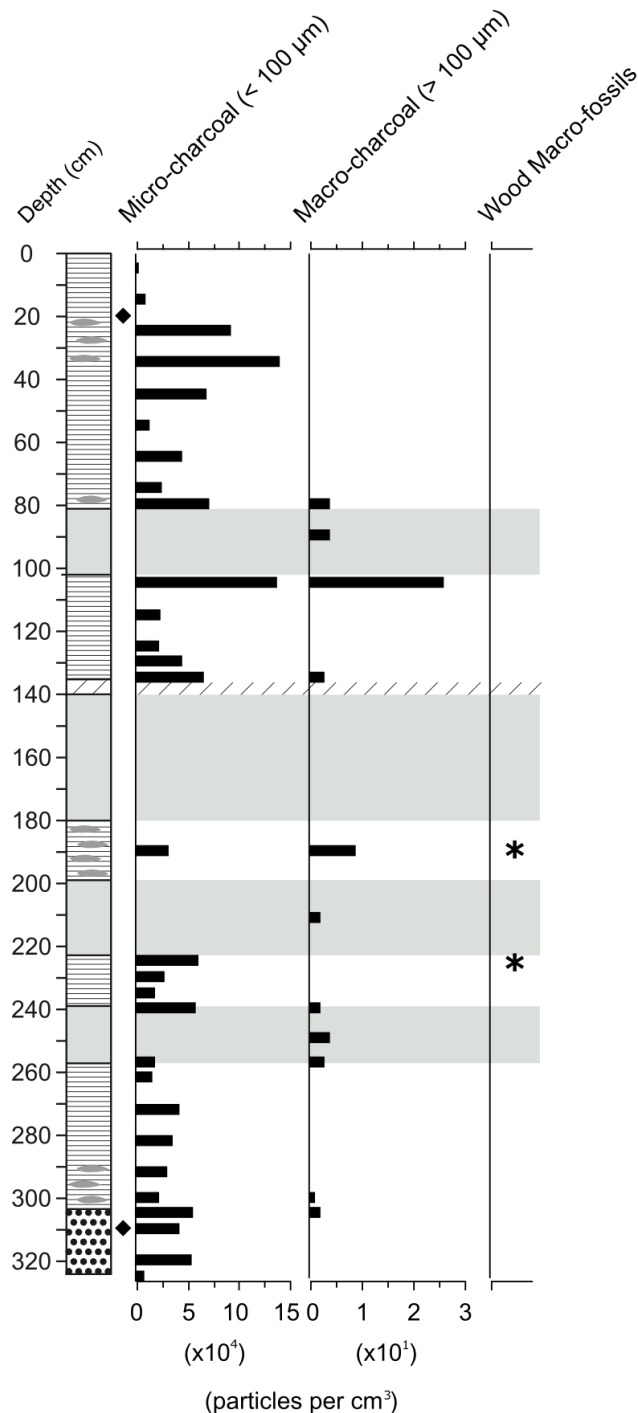


Figure 4.4 Micro- and macro-charcoal concentrations and wood macrofossils. Micro-charcoal (< 100 µm) and macro-charcoal (> 100 µm) are displayed as fragments per cm³. Asterisk (*) mark position of individual wood macro-fossil remains.

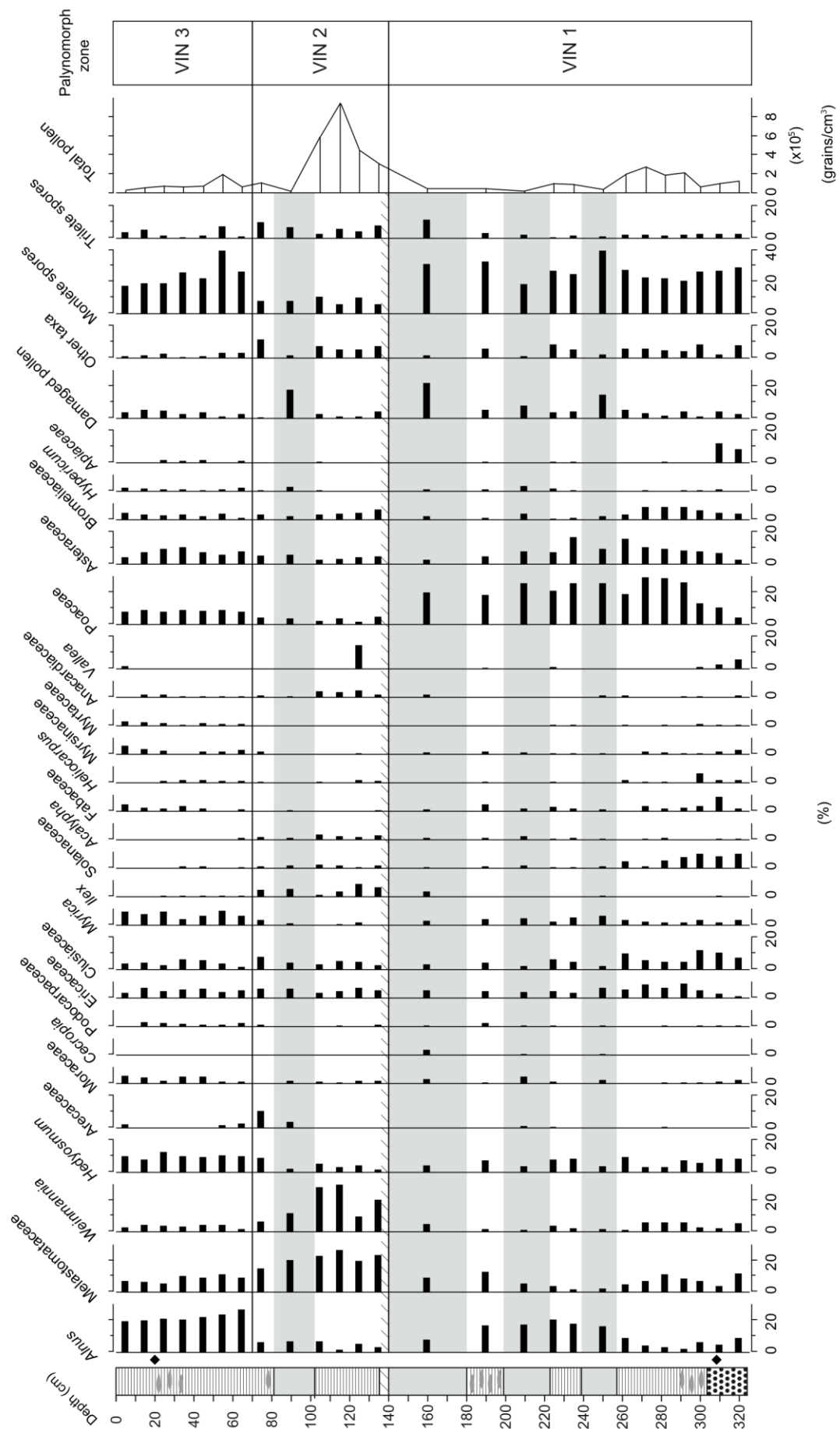
4.6.5 Palynomorphs

Zonation of pollen yielded three statistically significant stratigraphic zones, VIN 1 to VIN 3. (Figs. 4.5 and 4.6).

4.6.5.1 Pollen zone VIN 1

VIN 1 (13 samples, 320-140 cm) corresponds to SB and is characterised by abundant Poaceae (4-30 %) and fern spores (22-36 %). *Alnus* has a low abundance (2-9 %) at the base of the zone increasing after T4 to 7-21 %, while Solanaceae occurs at 1-9 % at the base of the zone and decreases after T4 to 0.3-1.4 %. Asteraceae (3-17 %), Melastomataceae (2-13 %), *Hedyosmum* (3-10 %), Ericaceae (1-9 %) and Clusiaceae (4-10 %) are consistently present but in low abundance. Pollen concentrations occur at 60,000-270,000 grains per cm³ at the base of the zone decreasing to 17,000-84,000 grains per cm³ after T4. The most abundant fungal NPP morphotypes in VIN 1 include HdV.123 (1-24 %), HdV.495 (1-19 %) and IBB.259 (1-14 %). The obligate coprophilous fungal spore *Sporormiella* is present in two samples in low abundance (< 3 %). *Coniochaeta* cf. *ligniaria* occurs in low abundances below T4 (0-6 %) increasing to 7-17 % in the beds containing wood macro-fossils. The semi-aquatic Cyperaceae fluctuate between 1-13 %. The lower part of the zone aquatic remains include *Isoëtes* (< 3 %), *Spyrogyra* (< 3 %), *Concentricystis* (< 8 %) and *Mougeotia* (< 5 %) and along with the sole aquatic zoological remains of HdV.179 (< 4 %). Above the lowest volcanic tephra layer aquatic remains are reduced with only *Spirogyra* (< 4 %) occurring in a single sample (Fig. 4.6).

Figure 4.5 (subsequent page) Fossil pollen and spore percentage diagram from Vinillos. Taxa include types that occur at > 2 % in at least one sample. Black diamonds indicate position of radiocarbon dates (Table 4.1)



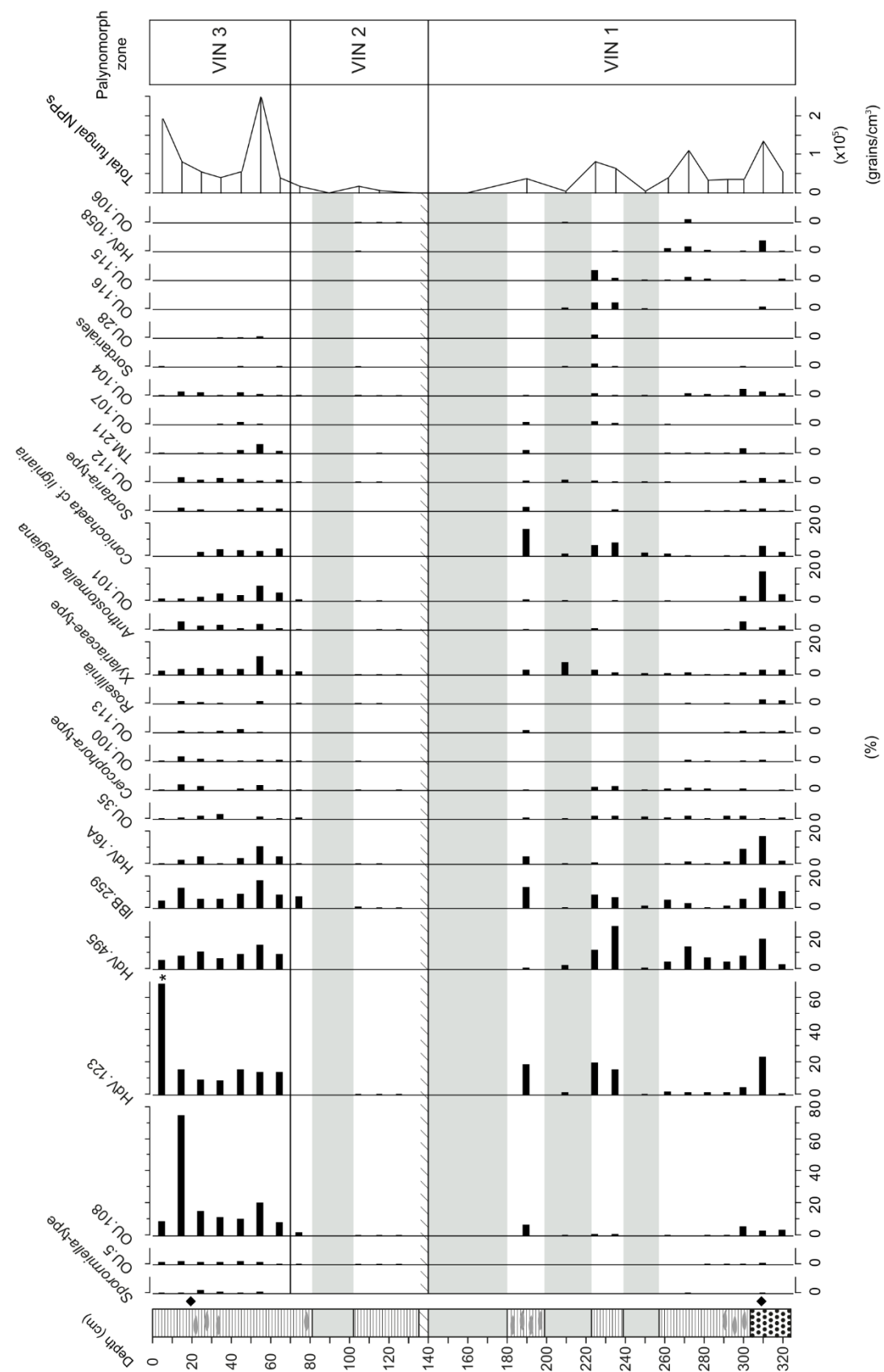


Figure 4.6 (*previous page*) Fossil non-pollen palynomorph diagram from Vinillos based on pollen percentage. NPP morphotypes represent types that occur at > 2 % abundance of the pollen sum in at least one sample. Asterisk (*) indicates count for morphotype HdV.123 in sample at 5 cm has been divided by 10 (687% of pollen sum). Black diamonds indicate position of radiocarbon dates (Table 4.1).

4.6.5.2 Pollen zone VIN 2

VIN 2 (6 samples, 140-75 cm) corresponds to SAO2, T1 and the lower most sample in SAO1 and is characterised by an abrupt decrease in the percentage of Poaceae (2-5 %), fern spores (12-17 %), *Alnus* (3-7 %) and Asteraceae (3-5 %). Melastomataceae (15-27 %), *Weinmannia* (6-27 %) and *Ilex* (1-8 %) increase along with a sharp increase in pollen concentration to 300,000-950,000 grains per cm³, with Melastomataceae and *Weinmannia* peaking at 251,000 and 282,000 grains per cm³ respectively in sample 115 cm, before dropping to < 110,000 per cm³ immediately at T1. Fungal NPP concentration is at its lowest point in VIN 2 (< 20,000 per cm³) and is effectively barren (< 10,000 per cm³) for 4 of the 6 samples within the zone. Semi-aquatic Cyperaceae are reduced occurring at 1-2 %, with aquatic elements *Isoëtes* (< 1 %) and *Spirogyra* (< 2 %) only present in single samples.

4.6.5.3 Pollen zone VIN 3

VIN 3 (7 samples, 75-0 cm) corresponds to SAO1 except for the lowermost sample and is characterised by an increase in *Alnus* (20-28 %), Myricaceae (3-9 %) and fern spores (18-41 %) in conjunction with a moderate increase in *Hedyosmum* (8-13 %), Asteraceae (4-11 %) and Poaceae (7-8 %). Melastomataceae (5-11 %), *Weinmannia* (< 5 %) and *Ilex* (< 1 %) all decrease. The pollen concentration is reduced again to that of VIN 1 (30,000-210,000 grains per cm³). Fungal NPP remains OU.108 (9-75 %), HdV.123 (9-690 %), HdV.495 (6-16 %) and IBB.259 (5-18 %) are the primary morphotypes with OU.108 dominant and HdV.123 hyper-dominant in the samples from 15 cm and 5 cm respectively. NPP concentration is highly variable in VIN 3 (ca. 40,000-250,000 per cm³) and reaches peak abundance in sample 55 cm. The obligate coprophilous fungi *Sporormiella* (0-3 %) returns in low abundance in VIN 3 appearing in a more continuous fashion. Semi-aquatic Cyperaceae increase (4-8 %) along with the return of more persistent aquatic elements *Isoëtes* (1-14 %), *Spirogyra* (0-33 %), *Concentricystis* (0-3 %) and *Mougeotia* (0-3 %).

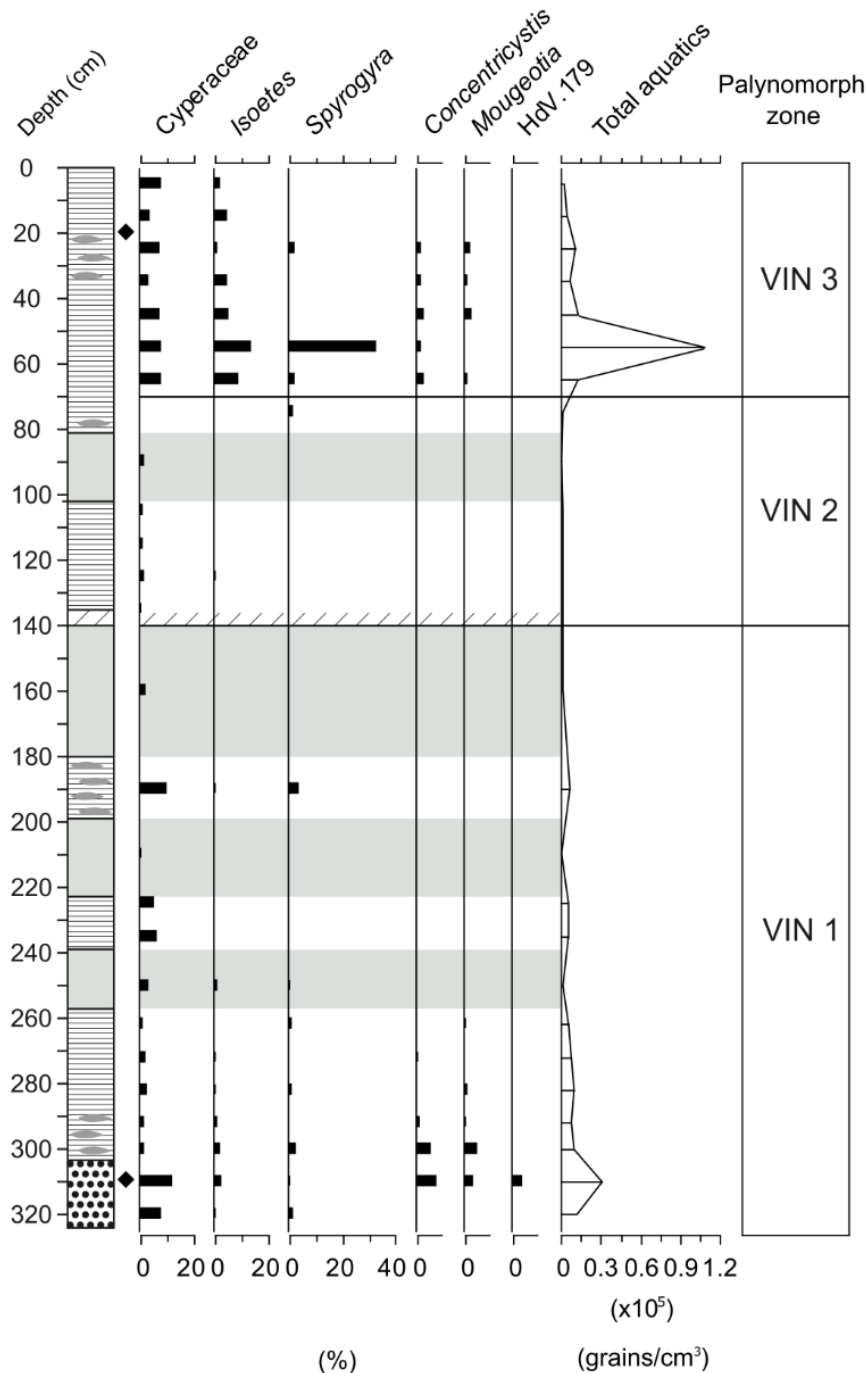


Figure 4.7 Fossil aquatic remains diagram from Vinillos based on pollen percentage. Remains include vegetative and zoological remains indicative of semi to fully aquatic conditions. Black diamonds indicate position of radiocarbon dates (Table 4.1).

4.7 Interpretation and Discussion

Calibrated radiocarbon dates from the top and bottom of the Vinillos section indicate that the sediments were deposited over a period of approximately 2,000 years between 44.3-42.7 ka (Table 4.1). Deposition of the sediments occurred between intervals of increased

precipitation during Heinrich events HE 4 (38.3-40.2 ka) and HE 5 (47.0-50.0 ka) (Sanchez Goñi & Harrison, 2010; Mosblech et al., 2012), within a period characterised by an oscillating climate corresponding to Dansgaard-Oeschger interstadials 11-9 (Blunier and Brook, 2001; Mosblech et al. 2012). Long sedimentary records from Andean lakes have shown vegetation responding to these climate fluctuations (van der Hammen and Hooghiemstra, 2003; Hanselman et al., 2011). These changes in climate likely contributed to vegetation change within the sedimentary snap shot at Vinillos, however, here I show that the often neglected non-climate drivers of vegetation change are vital in interpreting the past ecosystem dynamics driving landscape-scale change in the glacial montane forest of the eastern Andean flank.

4.7.1 Depositional Environment

The position of the Vinillos section near the base of an Andean valley suggests that deposition of the sediments took place in aquatic conditions on or near the valley floor. Fungal NPPs characteristic of swamp or bog conditions (HdV-123, HdV-16A) and the modern cloud forests (IBB.259) suggest deposition in a swamp or shallow water environment. Preservation of the sediments occurred as incision of a tributary of the Río Cosanga, now ca. 29 metres below the Vinillos section exposed the Vinillos sediments within the valley wall. Down cutting of the river is therefore calculated to occur at a rate of 6.9 mm per year between present day and the deposition of the youngest Vinillos sediments ca. 42 ka. This rate is at the upper end of predicted rates of denudation for eastern Andean montane rivers and is likely to reflect the high levels of precipitation that occur in the region (Aalto et al., 2006). No evidence of fluvial channel sediments have been identified in the Vinillos section sediments. The multiple volcanic tephra layers interbedded with the organic beds may have acted as a protective cap, preserving palynomorphs and wood macro-fossil remains from oxidation (Keen, 2015).

Aquatic pollen, algae and zoological remains preserved in the section signify the aquatic depositional environment of VIN 1 and VIN 3 (Fig. 4.6), with the highest proportion of aquatic remains occurring prior to the oldest volcanic tephra layer (T4) and subsequent to the youngest volcanic tephra layer (T1). This increase in the aquatic components may correspond to periods of reduced moisture availability during Dansgaard-Oeschger

interstadials 11-9, as observed in Lake Consuelo (Urrego et al., 2010). Aquatic remains become rare or absent during deposition of the four volcanic tephra layers, within VIN 2 and where lenses of volcanic ash occur within the organic sediments. This suggests that volcanic ash deposition may have led to inhospitable aquatic conditions during and immediately after its deposition, driving the changes in aquatic remains.

4.7.2 Glacial vegetation on the eastern Andean flank

The Vinillos section contains pollen taxa which are present within the modern pollen spectra of the eastern Andean flank, however, the fossil pollen assemblages are compositionally unlike any comparable modern pollen assemblage from the region (Cárdenas et al., 2014; Marchant et al., 2001; Rull, 2006; Weng et al., 2004b). This no-analogue pollen assemblage (*sensu* Williams and Jackson, 2007), indicates that a novel vegetation community existed at Vinillos during the late Pleistocene. The high abundance and association of typical Andean arboreal pollen taxa (e.g. *Alnus*, *Weinmannia*, *Hedyosmum*), presence of large wood macrofossils and low levels of Poaceae throughout the section (mean 13.5 %) are used to suggest a montane forest community was present during the deposition of the Vinillos sediments. Three pollen zones provide evidence for dynamic changes to the glacial forest pollen assemblage characterised by the dominance of Poaceae-Asteraceae-Solanaceae in VIN 1, Melastomataceae-*Weinmannia-Ilex* in VIN 2, and *Alnus-Hedyosmum-Myrica* in VIN 3. These changes in pollen assemblage through the Vinillos section are due to shifts in the abundance of particular pollen taxa and not the wholesale replacement of particular species, indeed every taxon except Myrtaceae and *Cecropia* can be found in each of the three pollen zones (Fig. 4.5). This change in pollen abundance between assemblages within a closed canopy moist tropical forests can indicate distinct changes in vegetation structure (Gosling et al. 2009, 2005). Pollen analysis from glacial Neotropical sedimentary archives have previously been used to conclude that millennial scale changes in temperature and moisture balance have driven vegetation change through the Quaternary (Colinvaux et al., 2000; Baker et al., 2001; Mourguiart & Ledru, 2003; Bush et al., 2004b; Urrego et al., 2005, 2010, 2016; Gosling et al., 2008; Bogotá-A et al., 2011; Groot et al., 2011). However, the cumulative effect of climate change on landscape-scale drivers such as increased precipitation leading to more frequent landslides is rarely discussed (Stern, 1995; Bussmann et al. 2008). Incorporating

landscape-scale drivers into past and future projections of vegetation change is essential in understanding how montane forest respond to environmental change. The three pollen assemblage shifts at Vinillos occurring over approximately 2 ka (44.3-42.6 ka) and in conjunction with volcanic tephra deposits suggest that non-climate factors can be the primary driver of short-term change in glacial montane forest communities. This pattern of population change is analogous to modern montane forest communities, where landscape heterogeneity, environmental variability and stochastic disturbance events lead to local variation in vegetation population within an identifiable vegetation zone.

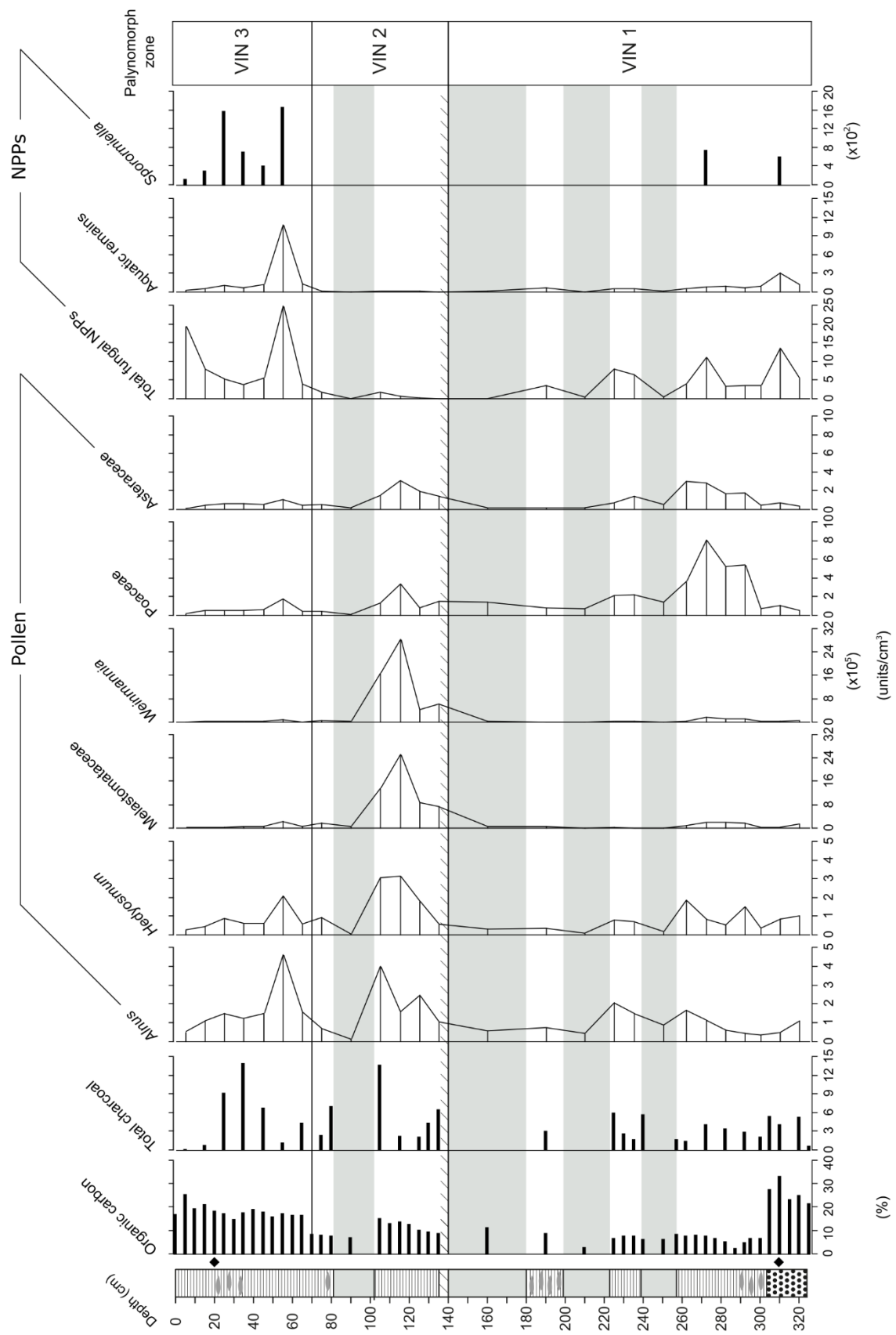


Figure 4.8 (*previous page*) Synthetic diagram of proxies used in reconstructing Vinillos section. Selected pollen taxa (*Alnus*, *Hedyosmum*, Melastomataceae, *Weinmannia*, Asteraceae and Poaceae), NPPs and charcoal are plotted as concentration per cm³. Organic carbon is plotted as a percentage. Black diamonds indicate position of radiocarbon dates (Table 4.1).

4.7.3 Landscape-scale drivers of vegetation change

4.7.3.1 Herbivory

Remains of Pleistocene megaherbivores such as giant ground sloths (Megatheriidae), armadillos (Chlamyphoridae) and Proboscideans (Gomphotheridae) have been found in the inter-Andean plain and lowland Amazonian rainforest of Ecuador (Marshall et al., 1983; Coltorti et al., 1998), but little evidence exists of herbivory within the steep slopes of the intermediate montane forest region. The Vinillos record contains low abundances (< 3 %) of the ascospore *Sporormiella*, an obligate coprophilous fungi which requires ingestion by herbivorous before being deposited in dung to complete its life cycle (Krug et al., 2004). *Sporormiella* has been used to determine changes in herbivore population and collapse during the late-Quaternary extinction (Davis, 1987; Gill et al., 2009), when large Pleistocene herbivores were likely important drivers of ecosystem change within the tropics (Corlett, 2013). The presence of *Sporormiella* at Vinillos suggests the local presence of herbivores along the valley floor within the glacial montane forest environment, but cannot provide further information on the type of herbivore or their abundance. The presence of small and large fauna may have contributed to seed dispersal, vegetation openness and hence fire reduction within the glacial montane forest environment.

4.7.3.2 Fire Regime

Fire is an important driver of vegetation change in the Neotropics (Bond & Keeley, 2005; van der Werf et al., 2008). However, high levels of year-round precipitation and ground level cloud within TMCF mean that they rarely burn naturally (Crausbay & Martin, 2016). The global fire regime has been shown to be diminished during glacial periods (Daniau et al., 2010), with Neotropical charcoal records containing reduced concentrations during the last glacial period (Mayle et al., 2009; Hanselman et al., 2011). Regional fires are indicated by the presence of micro-charcoal (< 100 µm) throughout the Vinillos sediments, however the

rare and limited concentrations (< 27 fragments per cm^3) of macro-charcoal ($> 100 \mu\text{m}$), which are indicative of local fires, suggests local burning was unlikely to have occurred (Whitlock & Larsen, 2001). The prevalence of burning in fire prone high elevation Páramo environments may indicate that charcoal fragments deposited at Vinillos were transported from this more combustible habitat (Coblentz & Keating, 2008; Hanselman et al., 2011). Vinillos is located between two active volcanos, Antisana (5704 m asl) and Sumaco (3990 m asl) (Fig. 4.1) (Hall et al., 2017). The co-occurrence of charcoal and tephra material throughout the Vinillos sediments suggests that volcanic eruptions were the likely ignition source of regional fires and that charcoal was transported to Vinillos during volcanic eruption events. The minimal macro-charcoal remains indicate that fires were not a major driver of vegetation disturbance within glacial montane forest environments.

4.7.3.3 Volcanic Activity

The response of an ecosystem to volcanic activity is linked closely to the type and quantity of volcanic material deposited. The volcanic tephra layers deposited at Vinillos are considered to be air fall deposits due to their fine-grained nature, however, some of the deposits may also have their origin in fine-grained material winnowed from pyroclastic flows. Each of the tephra layers contains low concentrations of pollen (15,000-48,000 grains per cm^3) and NPPs ($< 3,400$ grains per cm^3) similar in composition to their adjacent organic layers (Figs. 4.5 and 4.6) suggesting the period of deposition was long enough to incorporate a representative palynomorph signal or that the palynomorphs were transported within the tephra material.

The presence of three tephra layers within one pollen zone (VIN 1) indicates that the vegetation assemblage changed little after the deposition of T4 and T3. An increase in the proportion of *Alnus* pollen, a typical pioneer species in the Andes (Grau & Veblen, 2000; Weng et al., 2004a) within and adjacent to T4 and T3 indicates some disturbance of the forest community took place, but that no overall change in vegetation composition occurred. Pollen zone VIN 2 occurs immediately after the largest volcanic tephra layer (T2, 40 cm) and contains a change in the palynomorph assemblage to one characterised by high concentrations of *Weinmannia*, Melastomataceae and *Ilex* pollen, but an absence of fungal NPPs (Fig. 4.8). This shift in pollen assemblage and loss of fungal NPPs is interpreted to

indicate that the amount of volcanic ash deposited by T1, T2 and T3 caused the population dynamics and edaphic factors of the local area to change. Deposition of the youngest tephra layer (T1) coincides with a return to an assemblage comparable to that of VIN 1 with an increase in *Alnus*, *Hedyosmum* and *Myrica* (Fig. 4.5). Changes in the pollen zones through the Vinillos section broadly correspond to changes in sediment associated with the introduction of volcanic tephra material, indicating that volcanic activity is likely to have been an important driver of landscape scale ecosystem dynamics in glacial montane forest on the eastern Andean flank.

The occurrence of these non-climatic landscape-scale drivers (volcanic events, fires and herbivores) in conjunction with disturbance events which occur in modern montane environments, e.g. landslides, forest die-back, tree fall events, and presumably occurred in the glacial landscape allowed for stochastic local disturbances in the vegetation assemblages to occur (Fig. 4.8). These dynamic landscape scale processes led to local ephemeral vegetation assemblages occurring within the wider montane forest ecosystem. The persistent local level vegetation instability occurring through glacial climate regimes may have allowed for individual species to react quicker to climate driven vegetation change during the transition to an inter-glacial climate regime and potentially to cope with continued anthropogenic landscape degradation and future changes in climate.

4.8 Conclusions

The composition of the palynological assemblages through the Vinillos section indicates a stable regional vegetation community occurred on the eastern Andean flank of northern Ecuador during the last glacial period ca. 45-42 ka, despite landscape-scale processes driving local changes in forest structure. Deposition of volcanic ash was found to be the primary non-climate driver of landscape-scale changes in vegetation populations. Local vegetation population dynamics were driven primarily by these stochastic disturbance events, maintaining local vegetation heterogeneity during the last glacial period. No-analogue pollen assemblages from Vinillos indicate the presence of glacial forest communities that differ compositionally to the TMCF vegetation that occurs today, with higher abundances of characteristic montane taxa i.e. *Podocarpus*, *Alnus*, *Hedyosmum* and *Weinmannia*

indicating cooler conditions. The presence of obligate coprophilous fungi e.g. *Sporormiella*, provides evidence for the existence of herbivores within the glacial forest, however, low concentrations suggest they would have had a negligible impact on vegetation dynamics. The association between volcanic sediments and charcoal suggests that volcanic eruptions were the principle source of ignition in the Andes prior to the arrival of humans. Micro-charcoal observed in the record was likely transported from extra-local regions which were more susceptible to burning, e.g. Páramo, or entrained within ash falls. The paucity of macro-charcoal indicates that local fires were absent, or rare, within glacial montane forests.

4.9 Author contributions and acknowledgments

This chapter was written by Nicholas Loughlin (N.J.D.L.) with input and support of the supervisory team. N.J.D.L. prepared the samples, collected and analysed the data, wrote the chapter and created the figures. Radiocarbon dating was undertaken by Pauline Gulliver at the NERC Radiocarbon Facility East Kilbride (NRCF010001). Annemarie Philips (University of Amsterdam, Netherlands) provided assistance with sample preparation. Patricia Mothes (Instituto Geofísico, Escuela Politécnica Nacional, Ecuador) located the Vinillos site. Encarni Montoya and William Gosling along with Hayley Keen, Frazer Matthews-Bird and James Malley (all The Open University, UK) collected the Vinillos samples. As part of the submission of this chapter to the journal *Palaeogeography, Palaeoclimatology, Palaeoecology* two anonymous reviewers commented on the manuscript and provided constructive feedback which has been incorporated into this chapter.

Chapter 5

5 Assessing human impacts on the vegetation of the biodiverse eastern Andean flank before, and after, the arrival of Europeans (1492 CE)

5.1 Overview

In this chapter the response of tropical montane forest vegetation to changing human impact prior and subsequent to European arrival is assessed. This is then compared to pre-human and modern vegetation. This chapter is written as a manuscript in preparation for submission to the journal *Nature Ecology and Evolution*. The manuscript will be submitted in January 2018.

Loughlin, N.J.D., Gosling, W.D., Mothes, P., Montoya, E. Vegetation response to indigenous genocide on the Andean-Amazonian frontier.

5.2 Abstract

The tropical Andean region has been identified as a biodiversity hotspot that is vulnerable to degradation by growing human populations. However, little is known about the extent to which people modified these ecosystems in the past. An improved understanding of past human impacts on the biodiverse ecosystems of the Andes could provide useful insights for conservation into the likely consequences of the increasing pressure from modern human populations. Information on past human impacts can be obtained through examination of biotic and abiotic indicators contained within lake sediment that have accumulated over thousands of years. Here I present new data from the eastern Andean flank (Ecuador) that sheds light on the impact of human populations, pre- and post-European arrival (1492 CE), on the biodiverse cloud forest.

5.3 Introduction

The arrival of Europeans to the Americas had a catastrophic impact on the demographics and cultures of its indigenous peoples (Dobyns, 1966; Denevan, 2014). Prior to Spanish colonisation in South America indigenous populations were distributed across the Neotropics; however, the location, spatial scale, and intensity of pre-Hispanic human land-use remains contentious (Heckenberger et al., 2003; McMichael et al., 2012b, 2017; Clement et al., 2015; Goldberg et al., 2016; Levis et al., 2017). Evidence from archaeological (Porrás, 1975; Cuéllar, 2009), anthropological (Oberem, 1974; Newson, 1995; Uzendoski, 2004) and contemporary historical records (Medina, 1934) provide insight into the pre-Hispanic peoples of the Andean-Amazonian frontier. However, little is known about how historical changes in human population and land-use impacted the vegetation and ecosystem dynamics of this centre of biodiversity. The tropical montane cloud forests (1200–3800 meters above sea level (m asl)), located at the transition between the Andean mountains and Amazonia contain some of the most threatened ecosystems on Earth (Myers et al., 2000). The dense forests and steep slopes of the eastern flank of the northern Andes are not regarded as a major centre of pre-Hispanic culture, existing at the furthest extent of the Incan Empire (Newson, 1995). Here I present a new record of past ecological change and human impact obtained from lake sediments from the eastern Andean montane cloud forest of Ecuador. I reveal intensive land-use by pre-Hispanic indigenous people, and the

subsequent ecological response of land abandonment driven by the depopulation of the Quijos region during the genocide of its indigenous people.

Early excursions by Spanish conquistadors into the Ecuadorian Amazon (1538 CE; all dates hereafter in years CE) in search of gold, silver and cinnamon left from the city of Quito and travelled east over the Andes, through the Quijos Valley, and into the Amazonian lowlands (Newson, 1995; Uzendoski, 2004) (Fig. 5.1). In 1556 the conquest, religious conversion and establishment of '*encomienda*' (forced labour and tribute) of the Quijos chiefdom, with its population of ca. 35,000 indigenous people, was ordered by the Viceroy of Peru (Newson, 1995; Uzendoski, 2004). Spanish settlements were established throughout the region (Fig. 5.1). The Spanish town of Baeza was founded in 1559, near the indigenous settlement of Hatunquijos, within the Quijos Valley, an important trading centre between the Andean and Amazon peoples (Oberem, 1974; Newson, 1995). By 1576 Baeza contained an indigenous population of ca. 11,400 (Newson, 1995). However, forced labour, starvation, murder and brutal treatment of the indigenous peoples led to numerous uprisings (1560–1578), culminating in a final revolt and attack against the Spanish at Baeza, led by the "*great cacique Jumandi*" (Uzendoski, 2004). The revolt failed, subsequent reprisals and executions led many of the surviving inhabitants of the Quijos Valley to flee so that by 1600 the population of the town numbered less than 1000 (Newson, 1995; Uzendoski, 2004). Following the depopulation of the Quijos Valley and the destruction of towns within the wider Quijos region the Spanish in turn abandoned their colonial ambitions in the region (Uzendoski, 2004). The Quijos Valley remained virtually unpopulated for the next 250 years, so that even by the middle of the 19th century the former trading centre consisted solely of three small huts (Jameson, 1858; Orton, 1875).

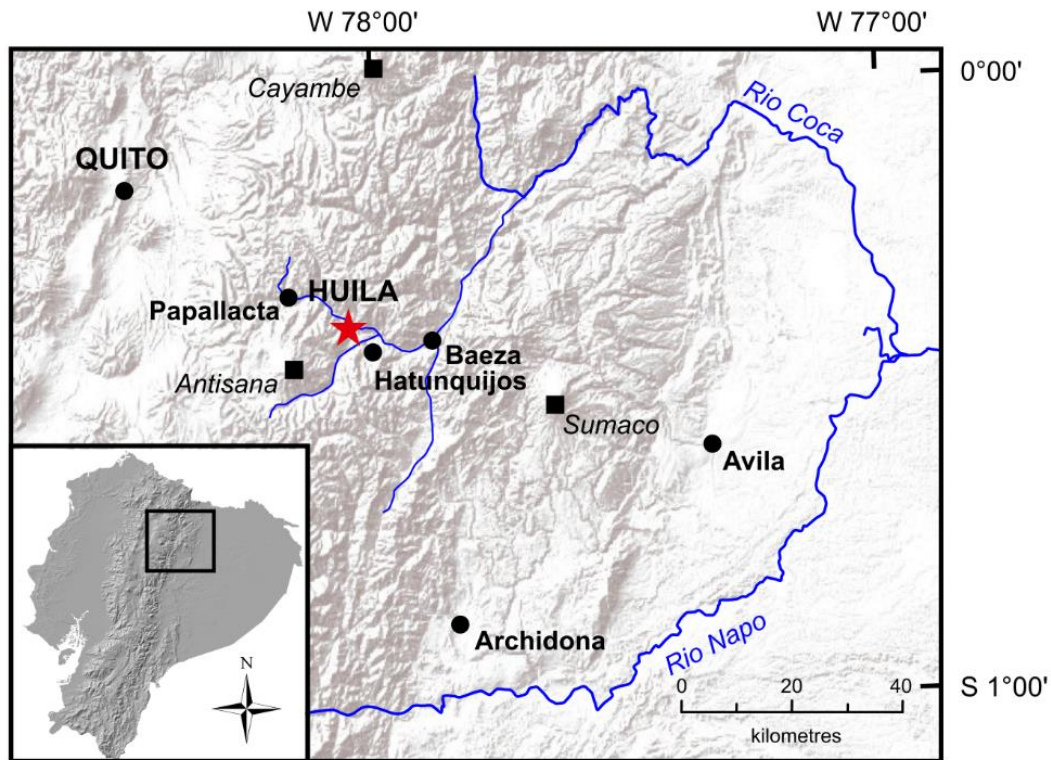


Figure 5.1 Map of study region. Indigenous Quijos region located on the Eastern Andean flank of Ecuador between the Rio Coca and Rio Napo. Black circles indicate present or past population centres. Black squares are active volcanos. Red star is location of Lake Huila.

5.4 Methods

Huila ($00^{\circ} 25.405' S$, $78^{\circ} 01.075' W$; 2608 m asl) is a small lake ($R = 15$ m) located on an isolated lava terrace within the Quijos Valley, underlain by volcanic rocks derived from the nearby Antisana Volcano (Hall et al., 2017) (Fig. 5.1; Appendix C). The Río Quijos, a tributary of the Río Coca and Río Napo, runs through the Quijos Valley a historically important trade route connecting the Andes to the Amazon (Medina, 1934; Oberem, 1974). Today Huila is located within a mosaic of open cattle pastures and secondary forest fragments most located on the steeper slopes of the valley. In 2013 two parallel sediment cores of up to 218 cm long were recovered from the centre of Huila using a Livingstone piston corer (Colinvaux et al., 1999). Pollen, non-pollen palynomorphs (NPPs), micro- and macro-charcoal were processed from the sediments using standard protocols (Colinvaux et al., 1999; Whitlock & Larsen, 2001) and analysed through the top 49 cm of the core above a 25cm thick volcanic ash layer. Pollen, NPPs and micro-charcoal were examined every 1-3 cm and macro-charcoal every 1cm. The volcanic ash layer is geochemically a dacite (Appendix C) and corresponds to

the eruption of Quilatoa ca. 1270, whose volcanic ash forms a regional marker layer (Mothes & Hall, 2008). Statistically significant palynomorph zones (pollen and fungal NPPs) were established using optimal splitting by information content, and the broken stick method in the program PSIMPOLL (Bennett, 2008). Detrended correspondence analysis (DCA) was then used to explore the terrestrial pollen and fungal NPP data from Huila, and plotted against an analogue for a structurally intact pre-human arrival montane cloud forest (Vinillos) and the modern human impacted secondary forest (Appendix Fig. 8.4). DCA was selected as an appropriate ordination technique as it produces a simultaneous ordination of the sample and taxa data maximising the correlation between samples, while compensating for the arch effect common in correspondence analysis and principle component analysis (McGarigal et al., 2000; McCune & Grace, 2002). Nonmetric multidimensional scaling (NMDS) provided similar results to the DCA, however, DCA was chosen over NMDS as its response to a strong primary gradient better visualised the dominant pattern in the data.

5.5 Chronology

A chronology for the upper 84 cm of the Huila core was established based on eleven accelerator mass spectrometry radiocarbon dates (Table 5.1). The Bayesian statistical package Bacon (Blaauw & Christen, 2011) was used in the “R” statistical computing package (R Core Team, 2015) to construct an age-depth model calibrated using the IntCal13 atmospheric curve (Reimer et al., 2013) (Fig. 5.2).

Table 5.1 Accelerator mass spectrometry (AMS) radiocarbon (^{14}C) dates of Huila palynomorph residues.

	Sample Identification	Sample Depth	Fraction modern carbon		Radiocarbon age	
			pMC	1 σ error	BP	1 σ error
1	D-AMS 017461	8cm	113.30	0.27	Modern	
2	D-AMS 017462	10cm	111.81	0.35	Modern	
3	D-AMS 017463	13cm	104.09	0.40	Modern	
4	D-AMS 017464	17cm	97.54	0.22	200	18
5	D-AMS 017465	19cm	98.77	0.38	99	31
6	D-AMS 017466	21cm	99.07	0.23	75	19
7	D-AMS 017467	24cm	95.67	0.22	356	18
8	D-AMS 017468	27cm	95.36	0.34	382	29
9	D-AMS 017469	42cm	94.49	0.34	455	29
10	D-AMS 017470	48cm	93.64	0.24	528	21
11	D-AMS 017471	84cm	87.73	0.29	1052	27

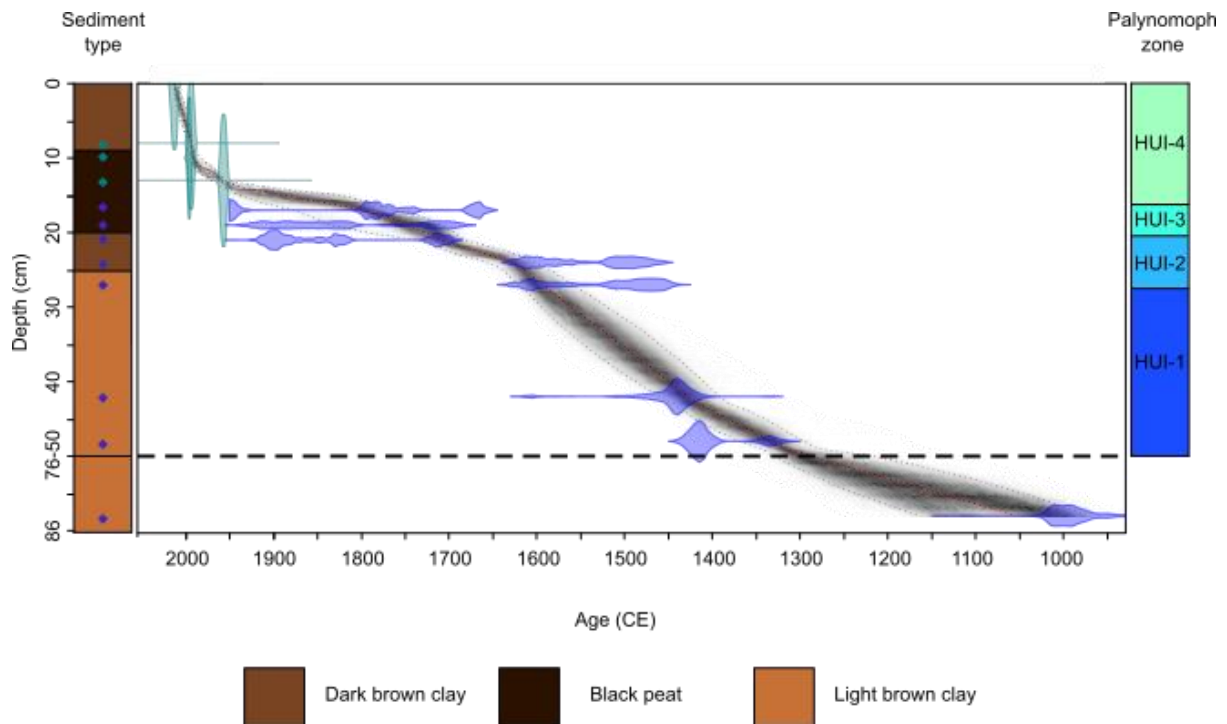


Figure 5.2 Age-depth model using Bayesian analysis. Dashed line (76-50 cm) represents a 26 cm volcanic tephra layer and is considered to have been deposited instantaneously.

5.6 Results

Palaeoecological proxy data revealed four distinct palynomorph zones representing distinct vegetation communities (Fig. 5.2). Pollen data was used to provide evidence of local (intra-basin, < 100 m) to regional (intra-valley, < 30 km) vegetation, and fungal NPPs as a proxy for local ecological processes. Macro- (> 100 μm) and micro-charcoal (< 100 μm) were used as evidence of local (< 100 m) to regional (< 30 km) burning within the Quijos Valley (Whitlock & Larsen, 2001).

Zonation of the palynomorphs show that HUI-1 extends from the pre-Hispanic period to ca. 1588, the late stages of indigenous revolt against Spanish rule. Sediments contain pollen primarily from herbaceous taxa (*Thalictrum*, Caryophyllaceae, Amaranthaceae) and some domesticated species (*Zea mays*). Fungal NPP type HdV.201 is the most common, with high levels of micro-charcoal and persistent low levels of macro-charcoal occurring in conjunction with spores of the charcoal loving fungi *Neurospora*.

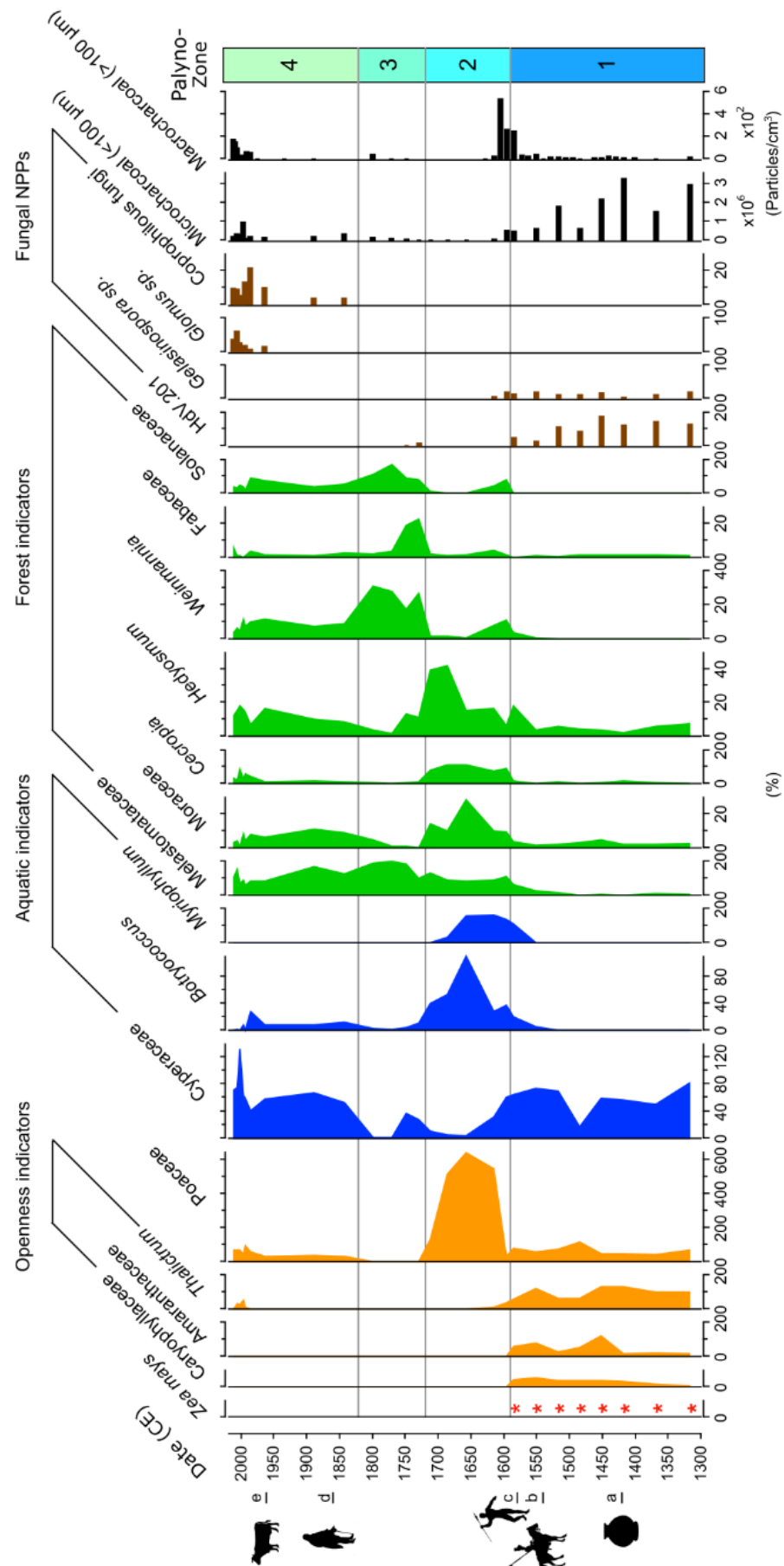


Figure 5.3 (*previous page*) Synthetic palaeoecological proxy diagram of Lake Huila core plotted against age. (a) Pottery shard recovered from core (42 cm), (b) Spanish arrival in Quijos region, (c) Indigenous uprising, (d) Post-colonial population and vegetation descriptions, and (e) the establishment of cattle farming in the region.

HUI-2 occurs between ca. 1588-1718 and sees an increase in the algae *Botryococcus* and aquatic pollen *Myriophyllum* occurring concurrently with a large spike in Poaceae. A single brief spike in macro-charcoal occurs at the interchange between HUI-1 and HUI-2, during the period of indigenous uprisings, but remains low throughout the rest of HUI-2 and throughout HUI-3 (ca. 1718-1819). Forest pollen percentage increases through HUI-2 and HUI-3 with a succession of pioneer and disturbance indicators (Poaceae and *Cecropia*) in HUI-2, followed by an increasing proportion of typical montane cloud forest taxa, such as Melastomataceae, Moraceae, *Hedyosmum*, *Weinmannia*, Fabaceae and Solanaceae in HUI-3 (Jørgensen & León-Yáñez, 1999). HUI-2 and HUI-3 occur concurrently within the period of low human population in the region ca. 1600-1850.

HUI-4 begins in ca. 1822 during the period of postcolonial Ecuadorian independence. Herbaceous pollen taxa e.g. Poaceae and Cyperaceae increase concomitantly with decreasing forest pollen taxa e.g. Melastomataceae and *Weinmannia*. Fungal spores associated with herbivore dung e.g. *Sporormiella* and *Podospora* occur for the first time, along with the mycorrhizal fungi *Glomus* ca. 1950, followed by an increase in micro- and macro-charcoal. HUI-4 occurs within the early stages of modern population expansion into the region and the conversion of montane cloud forest to pastures during the late 19th Century.

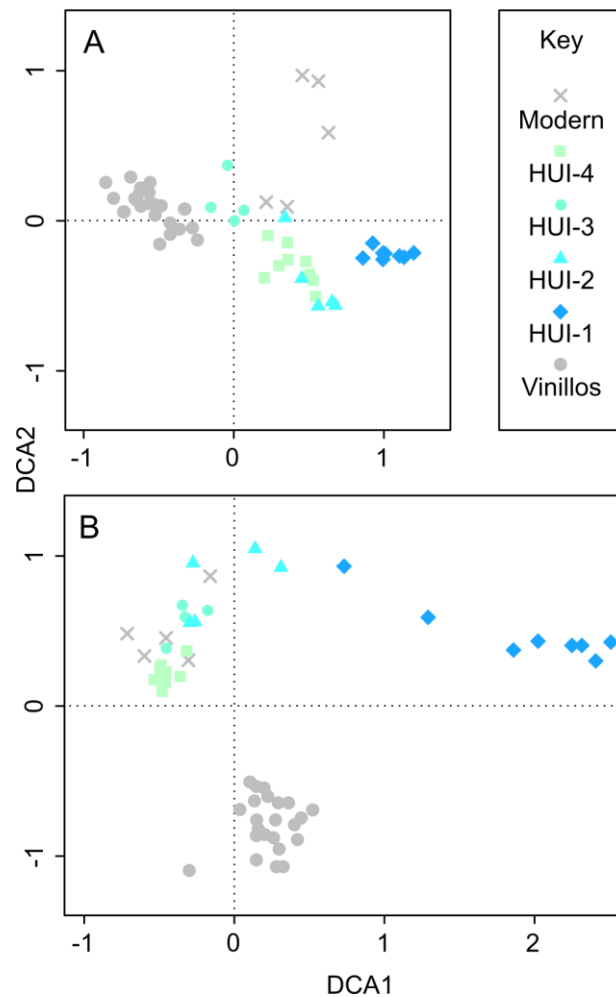


Figure 5.4 DCA of (A) pollen and (B) fungal NPP data. Blue through green colour ramp correspond to palynomorph zones from Huila. Grey circles are late-Pleistocene Vinillos samples. Grey crosses are modern surface samples (Appendix D).

5.7 Discussion and conclusions

In order to contextualise the palaeoecological record from Huila, proxy data were compared with the pre-human arrival (late-Pleistocene) sediments from Vinillos (Chapter 4), and surface samples obtained from local modern settings (Appendix D). DCA was used to visualise the relationships within the terrestrial pollen (Fig. 5.3A) and fungal NPP data (Fig. 5.3B). Five modern surface samples were taken from nearby secondary forest as indicators of palynomorph assemblages representative of recent human impact. Data from the Vinillos section (ca. 45-42 ka) was incorporated to represent an analogue of a structurally intact montane cloud forest prior to anthropogenic disturbance. DCA of pollen data (Fig. 5.3A) show that the signal from the pre-human arrival Vinillos assemblage is most similar to that

of the montane cloud forest that occurred between ca. 1718-1819 (HUI-3). The pollen signal from the modern mosaic landscape (HUI-4 and modern samples) is most similar to that of the secondary forest than occurred after the indigenous uprising (HUI-2). Fungal NPP data (Fig. 5.3B) show that along DCA axis-1, samples from all post-European contact settings i.e. modern samples, HUI-2, HUI-3 and HUI-4, are more similar to that of the pre-human arrival environment of Vinillos than that of the pre-Hispanic cultivated landscape (HUI-1).

The presence of *Zea mays* pollen in the Huila core at 84 cm indicates evidence of cultivation around Huila ca. 1054 (Appendix C), consistent with the earliest reliable pottery dates from Baeza ca. 972 (1151 ± 32 uncalibrated) (Cuéllar, 2009). Intact montane cloud forests rarely burns naturally (Bush et al., 2008), but the persistent presence of macro-charcoal and the charcoal loving fungal spore *Neurospora* in the pre-Hispanic Huila sediments, in conjunction with evidence of cultivation suggests that humans were the primary ignition source of local fires. High micro-charcoal abundance is used to infer ongoing regional fires within the Quijos Valley during HUI-1. The prevailing wind direction moving up the Andean flank would suggest the area around Hatunquijos (< 10 km east of Huila) as a likely source of regional fires. High proportions of herbaceous pollen taxa (e.g. *Thalictrum*, *Amaranthaceae*) and the fungal spore HdV.201, an NPP associated with helophytes (van Geel et al., 1989), suggests an open environment with humans as the primary driver of sustained clearance and land management during the period ca. 1287-1588 (HUI-1).

The transition from a pre-Hispanic cultivated landscape to secondary forest occurs abruptly ca. 1588. The depopulation of the Quijos Valley following the last major indigenous revolt (1577) coincides with a brief period of increased local burning around Huila as indicated by a brief increase in macro-charcoal by two orders of magnitude. Colonization by pioneer species occurs concurrently with the disappearance of crop species suggesting the abandonment of the cultivated land around Huila. A spike in grass pollen (623 % of the non-grass pollen sum), in conjunction with increasing aquatic elements (*Botryococcus* and *Myriophyllum*), have previously been shown to be indicative of floating aquatic mats (Bush, 2002; Bush et al., 2007). The increase in aquatic indicators are caused by changes in the hydrological conditions of the basin related to reduced landscape management and abandonment of the fields and terraces. Vegetation succession through secondary forest (HUI-2) to a montane cloud forest (HUI-3) occurs over approximately 230 years (ca. 1588-

1820), with little evidence of human impact observed during this period or recorded historically (Newson, 1995). The association of the pollen assemblages from the montane cloud forest (HUI-3) to that of the pre-human arrival Vinillos section (Fig. 5.3 A) shows that the forest recovery dynamics of a human impacted site converge with that of an intact Andean montane forest, supporting an equilibrium model of tropical forest recovery (Norden et al., 2009). However, this transformation from a managed, terraced pre-Hispanic cultivated landscape (HUI-1) to a montane cloud forest (HUI-3) alludes to the inability of Andean montane vegetation to recover to a structurally intact state within a period of less than 130 years (HUI-2, ca. 1588-1718).

Written accounts of the vegetation of the Quijos Valley from 1857 (Jameson, 1858) and 1867 (Orton, 1875) describe “a dense forest, impenetrable save by the trails” with few indigenous people. However, evidence of human impact on the vegetation during the post-colonial period is already seen to occur by ca. 1820 (HUI-4), indicating that even the impact of low human populations is recorded within the local pollen signal (Fig. 5.2). An increase in the proportion of herbaceous taxa and the first occurrence of coprophilous fungal spores at this time signifies the presence of herbivores (Davis & Shafer, 2006), and an increase in vegetation openness. Increasing coprophilous fungi and the presence of the mycorrhizal fungi *Glomus*, an indicator of increased basin erosion (van Geel et al., 1989), occurring ca. 1950 point towards an intensification of deforestation of the basin around Huila and the introduction of cattle farming. The absence of charcoal associated with the change from montane cloud forest (HUI-3) to forest mosaic (HUI-4) likely reflects the use of mechanical equipment for deforestation, opposed to the regular burning favoured previously.

The ecological proxies analysed throughout the Huila sediments (Fig. 5.2; page 88 and Appendix D; Figs. 8.6, 8.7, 8.8) and visualised within the ordination (Fig. 5.3) allow for the comparison of the pre-Hispanic cultivated landscape with that of the modern mosaic landscape. Today Huila is approximately 500 m from the nearest stand of secondary forest, although occasional lone trees covered in epiphytes do grow within the surrounding pasture. The paucity of forest pollen, abundance of micro-charcoal and unique NPP assemblage indicative of an open landscape in the pre-Hispanic sediments advocates for an environment with fewer trees, more highly managed, and with a landscape more degraded than that of the mosaic landscape we see today.

The postcolonial population of the Quijos region only exceeded that of the pre-Hispanic population by the end of the 20th Century (Appendix C), with widespread deforestation and the establishment of cattle farming seeing vast areas of montane cloud forest in Ecuador disappear. However, the intensity of pre-Hispanic human impact is shown to have locally exceeded that of current vegetation degradation. The genocide of the indigenous people of the Quijos Valley during European colonisation saw the switch from a pre-Hispanic cultivated landscape to that of a secondary forest by ca. 1588, transitioning to a montane cloud forest within 130 years (ca. 1718).

5.8 Author contributions and acknowledgments

This chapter was written by Nicholas Loughlin (N.J.D.L.) with input and support of the supervisory team. N.J.D.L. prepared the samples, collected and analysed the data, wrote the chapter and created the figures. N.J.D.L., Encarni Montoya and William Gosling collected the Huila and modern samples. Radiocarbon dating was undertaken by Pauline Gulliver at the NERC Radiocarbon Facility East Kilbride (NRCF010001). Annemarie Philips (University of Amsterdam, Netherlands) provided assistance with sample preparation. Patricia Mothes (Instituto Geofísico, Escuela Politécnica Nacional, Ecuador) located the Huila and Vinillos sites. Encarni Montoya and William Gosling along with Hayley Keen, Frazer Matthews-Bird and James Malley (all The Open University, UK) collected the Vinillos samples. As part of the submission of this chapter to the journal *Nature Ecology and Evolution* Crystal McMichael (University of Amsterdam, Netherlands) commented on the manuscript and provided constructive feedback.

Chapter 6

6 Discussion and conclusions

6.1 Overview

Chapter 6 directly addresses the five research aims laid out in Chapter 1 and that were investigated in Chapters 3-5. The overriding research question is examined and its wider implications to contemporary work discussed. Conclusions are stated and potential future work proposed.

6.2 Introduction

The first humans arrived in South America ca. 18.5-14.5 ka, making it the last habitable continent to be colonized (Dillehay, 2009; Reich et al., 2012; Dillehay et al., 2015; Raghavan et al., 2015). People spread rapidly throughout the region, but populations remained low until sedentary behaviour became widespread ca. 5 ka (Reich et al., 2012; Goldberg et al., 2016). Research into the history of human-landscape interactions in the western Neotropics

has until recently concentrated primarily on the Pacific coastal region, where the oldest evidence of human habitation exists (Piperno & Stothert, 2003; Stothert et al., 2003; Dillehay et al., 2007, 2008, 2015, 2017) and within the inter-Andean valley where the great Andean civilizations arose (Chepstow-Lusty et al., 1996, 1998, 2009; Kolata, 1996; Erickson, 1999, 2000a; Williams, 2006; Bauer & Kellett, 2010). The impact of pre-Hispanic humans on the Amazon was initially considered to be minor due to poor soils limiting intensive agriculture (Meggers, 1954). However, large areas of organic rich soil containing high concentrations of human deposited inorganic (charcoal, pottery sherds, animal bones) and organic (biomass wastes, manure, excrements, biochar) material, referred to as Anthropogenic Dark Earths or *terra preta*, were subsequently discovered (Lehmann et al., 2007; Glaser & Birk, 2012). Archaeological and palaeoecological studies have corroborated this evidence pointing towards the presence of permanent communities with complex agricultural, political and socio-economic structures (Erickson, 2000b; Carson et al., 2014; Watling et al., 2017). This indicates that the densely forested Amazon was in fact a mosaic of variably human impacted environments (Heckenberger et al., 2003; McMichael et al., 2012a, 2012b, 2017; Clement et al., 2015; Levis et al., 2017).

The research undertaken in this thesis expands on our understanding of the role that pre-Hispanic indigenous peoples played in driving ecosystem dynamics in tropical South America. Here the long-term (> 100 years) impact of human populations at the cultural and ecological frontier dividing the Andean mountains from the lowland Amazon rainforest is investigated. Understanding how these tropical montane forests have responded to changing human impact through time offers us the opportunity to ascertain how one of the most biodiverse yet endangered habitats in the world may respond to ongoing and future human driven environmental degradation. Viewing past ecosystem dynamics and vegetation recovery in the palaeoecological record offers a chance to establish goals or ecological baseline from which conservation and restoration strategies can be assessed.

The steep, wet, densely forested, dynamic landscape of the eastern Andean flank of Ecuador has in the past been seen as unfavourable to extensive pre-Hispanic occupation and the impact of its indigenous peoples on the vegetation prior to European arrival overlooked (Means, 1931). The heterogeneous landscape, periodic volcanic activity and regular landslides prohibit the formation of ancient lakes on its steep slopes, leading to a paucity of

suitable sites from which palaeoecological studies could proceed. Some archaeological and historical evidence points to pre-Hispanic indigenous occupation on the eastern Andean flank (Porras, 1975; Newson, 1995; Marín, 2002; Uzendoski, 2004; Cuéllar, 2009), however, little is understood of the extent and impact that these populations may have had on the vegetation through time. In this thesis I contribute two new sites (Vinillos and Huila) to the ongoing investigation of past vegetation change and human impact within the Neotropics.

6.3 Research aims

Chapter 1 outlined the five research aims to be addressed in this thesis. These aims were established in order to characterise the response of Andean montane forest vegetation to landscape-scale drivers of ecosystem change through time. The outcome of these research aims are reached within the data chapters (Chapters 3-5), and are here summarised and discussed:

6.3.1 Research aim 1: Characterise changes in non-pollen palynomorphs across a gradient of montane forest cover

Fungi perform a vital function in terrestrial ecosystems as, among other roles, they are symbionts and decomposers of vegetation. Due to this role a relationship exists between plant and fungal communities (Hooper et al., 2000; Peay et al., 2013). Analysing fungal remains across ecological gradients offers the potential to assign distinct fungal assemblages to particular vegetation communities, a valuable tool in understanding past ecosystem dynamics. Modern analogue studies have previously shown a relationship with vegetation communities across the tropical Andes (Grabandt, 1990; Montoya et al., 2010, 2012). However, relating NPPs to environmental gradients on the eastern Andean flank presents a particular challenge. The dynamic nature of the landscape means there are few suitable study sites from which samples can be recovered (e.g. lakes or swamps) for the generation of a modern training dataset. Switching to alternative sources of samples (e.g. surface soil, moss polsters or artificial traps) is often not optimal for studying NPPs as the signal obtained is very local and consequently not representative of the wider environment. To overcome this challenge two study sites were selected on the eastern Andean flank from which a

series of samples deposited in aquatic settings through time were recovered. This method allowed for the control of the depositional environment, with snap-shots of vegetation in time, rather than space, used as the factor separating samples along an ecological gradient.

A quantitative assessment of forest pollen taxa and fungal NPPs was undertaken (Chapter 3) in order to determine the relationship between NPP assemblage and forest cover. NPP zones were established using optimal splitting by information content and the statistical significance of zones tested using the broken stick method. This process established three fungal NPP zones corresponding to forest pollen taxa characterised as containing, low (< 8 %), medium (8-32 %), and high (32-63 %) levels of forest cover. This novel approach allowed for changes in fungal NPP assemblages across a gradient of montane forest cover to be assessed while reducing the sample bias effect and solving the problem of a lack of suitable sampling locations.

Zonation along the forest cover gradient indicated that the only statistically significant boundary occurred separating the low forest cover zone from that of the medium-high forest cover zones, at ca. 8 % forest pollen. The low forest cover NPP assemblage is characterised by types such as *Neurospora*, IBB-16, HdV-201, OU-102 and OU-110. This separation of the samples representing low forest cover was also observed within the DCA of fungal NPPs (Fig. 5.3; page 89). Therefore, a distinct NPP assemblage can be used to characterise an open eastern Andean montane environment with limited forest cover. Long-term records of mid-elevation montane vegetation on the eastern Andean flank have consistently shown that forest taxa have dominated the landscape throughout the Quaternary (Urrego et al., 2005, 2010; Cárdenas et al., 2014; Keen, 2015). Therefore, the low proportion of forest pollen taxa and its corresponding distinctive NPP assemblage indicates that periods of low forest cover, such as during periods of deforestation are reflected within the local fungal community.

6.3.2 Research aim 2: Identify the environmental drivers of fungal non-pollen palynomorphs within the montane forest environment.

NPPs consist of a variety of preserved organic remains (plant, fungal, algal, zoological) capable of characterising changes in ecosystem dynamics. Fungal NPPs have been used

successfully to establish past trends of anthropogenic impact (van Geel et al., 2003; López-Sáez & López-Merino, 2007; Williams et al., 2011; Doyen & Etienne, 2017), provide evidence of herbivore extinctions (Davis, 1987; Gill et al., 2009, 2013), and their role shaping landscapes (Davis & Shafer, 2006; Raper & Bush, 2009; Baker et al., 2013, 2016). As such understanding the relationship between fungal NPPs and the variables that influence them offers the potential to greatly increase the effectiveness of this proxy in reconstructing past environments.

A host of environmental and ecological variables act as important drivers on fungal NPP distribution and abundance. In Chapter 3, proxies for four variables, forest pollen taxa (forest cover), aquatic remains (available moisture), micro-charcoal (regional fire regime), and organic carbon (sediment composition), were used to provide environmental gradients against which to constrain the autoecological characteristics of the fungal NPPs encountered. Using the sedimentary archives as a training data set allows us to explore assemblage shifts along longer environmental gradients than would be possible using just modern samples in the Andes. Canonical Correspondence Analysis (CCA) was used to plot the known and unknown fungal NPP types against the environmental variables. This method of data visualisation allowed for the potential autecological information of the fungal types to be interpreted based on how they covary with the environmental gradients and indicate the most important explanatory variable (environmental gradient). Analysis of variance (ANOVA) was used to test the significance of the variance in the fungal NPPs explained by the environmental gradients. The explanatory variables were shown to account for ca. 40 % (constrained inertia = 0.8187) of the variance in the dataset (total inertia = 2.0438), with the first two CCA axis accounting for 90 % of the explained variance (Eigenvalues CCA1 = 0.4235, CCA2 = 0.3198). This indicates that environmental variables not parameterised here (e.g. climate, direct human disturbance, edaphic factors, plant-fungal interactions) have an important influence on assemblage composition.

Fire was found to be the most important explanatory variable of fungal NPP assemblage composition, with available moisture and sediment composition the next most important factors (Section 3.7.3). The relationship between forest cover and NPP assemblage was poorly resolved, despite the strong relationship between low forest cover and a distinctive NPP assemblage identified in the previous research aim. These seemingly contradictory

aspects maybe explained by the relationship observed between forest cover and fire. Fig. 3.4 (Section 3.7.3) displays the inverse relationship between the fire and forest cover gradients, indicating that more open environments burn more frequently than forested environments. The presence of the taxa indicated to be linked to the low forest cover gradient above (*Neurospora*, IBB-16, HdV-201, OU-102 and OU-110) covary with the fire gradient, supporting this relationships and distinct NPP assemblage.

6.3.3 Research aim 3: Determine the fire regime in montane forests prior to the arrival of humans.

Tropical montane forests located in areas of high orographic rainfall are persistently wet and in the modern environment rarely burn naturally (Urrego et al., 2010; Bush et al., 2011). Lightning strikes may initiate small fires, however, these are liable to burn out within the wet understory (Alencar et al., 2004). Volcanic eruption can lead to extensive burning within the Páramo which covers the upper flanks of some Andean volcanos, however, burning is generally restricted to above the tree line, barring large pyroclastic flows and lava eruptions penetrating the upper forest. Today fires within montane forests are linked directly with human activity, primarily associated with the clearance of vegetation for the purpose of cultivation and pastures. Evidence from long palaeoecological records from the eastern Andean flank disagree as to the importance of fire prior to the arrival of humans, with some records containing no evidence of fire for thousands of years (Urrego et al., 2005, 2010), while others suggest that it may have been a natural disturbance factor initiated by volcanic activity (Cárdenas et al., 2014).

In order to determine the importance and ignition source of the non-human initiated fire regime of the study region sediments from the late-Pleistocene Vinillos site were analysed for macro- ($> 100 \mu\text{m}$) and micro- ($< 100 \mu\text{m}$) charcoal fragments. Results indicate that local and extra-local fires were likely to be rare or absent within the montane forest, but may have occurred in conjunction with volcanic activity. Increased micro- charcoal concentrations covary with the volcanic tephra layers at Vinillos, suggesting aerial transportation of micro-charcoal entrained within volcanic ash, likely representing regional burning that occurred in proximity to the eruption points. The limited macro-charcoal fragments that do occur within the sediments, are below the minimum limits suggested to

indicate local fires (Whitlock & Larsen, 2001). These macro-charcoal fragments may have also been transported by large convective columns from fires outside the local montane forest, or may represent fragments transported overland after increased erosion following the deposition of ash layers. This suggests that fire at the Vinillos location was not a major driver of vegetation change within the glacial montane forest ecosystem and that even when associated with its primary ignition source (volcanic eruptions) was likely to contribute little to ecosystem dynamics during the deposition of 10's of cm of volcanic ash. This absence of significant levels of macro-charcoal and low levels of micro-charcoal even during periods of volcanic activity suggests that evidence of substantial burning within the montane forest after human arrival is likely associated with human activities. However, the presence of charcoal on its own cannot be used as proof of human initiated fires. Changes in climate during periods of early human occupation, e.g. increased temperature during the mid-Holocene dry event, may have contributed to the likelihood of natural burning taking place within the montane forest.

6.3.4 Research aim 4: Assess the drivers of landscape-scale ecosystem dynamics prior to human influence on the montane forest environment.

Few palaeoecological studies have been undertaken within the montane forests of Ecuador due to its dynamic nature leading to a paucity of ancient preserved sediments. Palynological analysis of discontinuous sediments from cliff sections at Mera, Erazo and San Juan de Bosco sites indicate changing forest assemblages through the Quaternary were driven primarily by long-term (millennial) changes in climate (Liu & Colinvaux, 1985; Bush et al., 1990; Colinvaux et al., 1997; Cárdenas et al., 2011, 2014; Keen, 2015). However, research into the role of non-climate drivers of vegetation change in this setting has been limited (Cárdenas et al., 2014). Understanding the role of these processes prior to the arrival of humans to the continent is essential in order to understand the impact people have played on modifying the landscape and in attempts to establishing natural ecological baselines.

The late-Pleistocene sedimentary sequence at Vinillos, located within the montane forest of the eastern Andean flank of Ecuador offered the prospect of identifying the non-climate drivers of vegetation change prior to the arrival of humans to the Americas. A multiproxy analysis (pollen, non-pollen palynomorphs, charcoal, geochemistry and carbon content) of

the sediments was used to provide a snap shot of the vegetation community and determine the role of three important landscape-scale drivers of ecosystem dynamics (volcanic activity, fire regime and herbivory) (Fig. 4.8; page 77)

Pollen analysis from Vinillos indicated the presence of a glacial forest community that was non-analogous to that of the tropical montane cloud forest vegetation that occurs today, with greater proportions of montane taxa characteristic of higher altitudes i.e. *Podocarpus* and *Weinmannia*, indicating cooler conditions. The presence of obligate coprophilous fungi e.g. *Sporormiella*, provided evidence for the existence of herbivores within this glacial forest, however, low concentrations suggest they would have had a negligible impact on the vegetation. The association between volcanic sediments and charcoal suggests that volcanic eruptions were the principle source of ignition in the Andes prior to the arrival of humans, however, as discussed above, fire was uncommon and unlikely to have been a major driver of ecosystem dynamics. Volcanic activity, primarily the deposition of volcanic ash was determined to have been the most important non-climate driver of landscape scale vegetation change.

The ash layers within the Vinillos sediments range from several millimetres to ca. 40 cm thick, however, the palynomorph assemblages change after two deposition events. The first is the deposition event is that of tephra layers T1, T2, T3. This event is suggested to have been a prolonged period of ash deposition and organic material transportation. Evidence of palynomorphs within the ash layers and large wood macro remains within the inter-bedded organic material suggest deposition during a period of intense volcanic activity and landscape modification, culminating in the ash fall of T3. This is followed by the volcanic event at T4 where 18 cm of ash material is deposited and is followed by a distinct change in the pollen and NPP assemblages. The changes in the pollen signal in conjunction with the tephra deposits shows that the local population dynamics responded to these stochastic events, however, the composition of pollen taxa remains consistent through the section, despite changes in the abundance of some taxa (Fig. 4.5; page 71). This suggests that despite physical perturbations, the regional vegetation community present on the eastern Andean flank during the last glacial period ca. 45-42 ka BP was compositionally stable and able to recover from local perturbations.

6.3.5 Research aim 5: Establish the ability of pre-Hispanic indigenous peoples to impact the montane forest of the eastern Andean flank.

The Quijos Valley is one of the few accessible routes connecting the high Andes to the Amazon in northern Ecuador. Archaeological and historical evidence suggests that the valley acted as important trade routes between the Incan empire and the peoples of the Amazonian lowlands prior to European arrival (Uzendoski, 2004; Cuéllar, 2009). However, the dense montane forests was long considered unsuitable for habitation by large pre-Hispanic populations (Means, 1931). Lake Huila is located between the Spanish town of Baeza and the indigenous settlement Hatunquijos within the Quijos Valley, providing the ideal location to explore the impact of changing human population on the montane forest of the eastern Andean flank prior and subsequent to European contact.

Multiproxy palaeoecological analysis (pollen, NPP, charcoal, LOI) of the Huila sediments reveal a distinct vegetation community during the pre-Hispanic period. The basal palynomorph zone (HUI-1) extends from the pre-Hispanic period to ca. 1588 CE. The earliest evidence of human presence being based on the occurrence of *Zea mays* pollen ca. 1054 CE (Appendix C: Fig. 8.3 sample at 86 cm) and a pottery sherd dated to ca. 1423 CE (Fig. 5.2; page 88). The presence of *Zea mays* and pollen primarily of herbaceous taxa (*Thalictrum*, Caryophyllaceae, Amaranthaceae) indicate an open environment with some degree of cultivation. Persistent micro- and macro-charcoal, and the presence of the charcoal loving fungal spore *Neurospora* prior to European arrival suggest fires were frequent (Fig. 5.2; HUI-1), and as intact montane cloud forests rarely burn naturally, humans were the likely source of ignition.

The DCA of samples from all periods indicate that the pre-Hispanic sediments form distinctive pollen and fungal NPP assemblages (Fig. 5.3; page 89). The segregation is observed when the forest cover proxy (forest pollen percentage) is plotted against NPPs in Fig. 3.3 (pages 47-48), lumping the pre-Hispanic samples into a statistically significant assemblage representing < 8 % forest pollen and characterised by the types *Neurospora*, IBB-16, HdV-201, OU-102 and OU-110. CCA of the fungal NPPs (Fig. 3.4; page 51) indicate that these characteristic NPP types covary with the fire environmental gradient, which exhibits an inverse relationship to forest cover. This evidence, provided by the

palaeoecological proxies indicate that the pre-Hispanic landscape was characterised by novel pollen and NPP assemblages indicative of an open cultivated landscape where fire was an important ecosystem driver of ecosystem dynamics.

6.4 Discussion

The principal goal of this thesis was to determine how the biodiverse tropical montane forest of the eastern Andean flank has responded through time to changes in human impact. The Quijos Valley was chosen as an appropriate test case for this study due to its archaeological and historical record of indigenous occupation prior to European arrival and its history of colonisation and indigenous depopulation. In this thesis four phases, characterised as: 1) pre-Human arrival (control), 2) pre-Hispanic indigenous occupation, 3) European colonization, and 4) post-independence modern habitation, are examined. Phases 2 and 3, and the transition between them are used to address how the biodiverse tropical montane forest responded to an abrupt change in human impact. Phase 1 and 4 act as references in which to view these changes. Phase 1 representing a natural or intact forest environment prior to human arrival on the continent and phase 4 representing a degree of human impact that can be observed today in the modern environment. Establishing the historical interaction between an ecosystem and its human inhabitants will allow this research to frame future assessments of ecosystem services and provide a long-term perspective for conservation and restoration strategies in one of the most biodiverse and threatened habitats in the world.

6.4.1 Vegetation response at European arrival on the eastern Andean flank

The ability of pre-Hispanic indigenous people to modify the landscape and vegetation in forested lowland environments has been well documented (Erickson, 2000b; Heckenberger et al., 2008; Schaaf et al., 2012; Carson et al., 2014; Watling et al., 2017), with evidence of cultivation in the Amazon extending back at least 6000 years (Bush et al., 1989, 2016). However, the heterogeneous distribution of the pre-Hispanic indigenous population means that quantifying the impact of humans across the Neotropics prior to European arrival is exceptionally difficult (Dobyns, 1966; Reich et al., 2012; Denevan, 2014; Clement et al.,

2015; Goldberg et al., 2016). Archaeological studies indicate that past human populations centres were often concentrated near the coast, waterways, topographic features and in regions with more productive soils (McMichael et al., 2012a, 2017; Piperno et al., 2015). These sites still often contain evidence of distinctive vegetation change, such as a high abundance of cultivated or *useful* (to people) species (Heckenberger et al., 2003; Clement et al., 2015; Levis et al., 2017). Modern vegetation studies continue to struggle to identify the long-term impact of human activity on the composition and structure of tropical forests, or identify 'pristine' forests. This has led to continuing debate as to the changing role of humans as the primary driver of past vegetation change through time (Denevan, 1992, 2016; Heckenberger et al., 2003).

The Huila sedimentary sequence records the changing impact of humans on the montane forest vegetation of the eastern Andean flank from the pre-Hispanic period to today. Archaeological evidence and historical documentation suggests that the Quijos Valley has played an important role as a trade route between the Andes and western Amazonia throughout this period (Newson, 1995; Uzendoski, 2004; Bray, 2005; Cuéllar, 2009). Historical records indicate it was the main route over the eastern Andean flank from the historical capital of Quito into the Amazon, for not only the pre-Hispanic indigenous peoples but also the invading Europeans (Bray, 1995; Newson, 1995; Uzendoski, 2004). Archaeological and written evidence of the local indigenous peoples, indicate that they lived in the valley at Hatunquijos prior to European arrival (Fig. 5.1; page 86 and Appendix C; Fig. 8.2). In 1559 CE Spanish conquistadors and colonial settlers established the town of Baeza at the head of the Quijos Valley near Hatunquijos (Newson, 1995; Uzendoski, 2004; Cuéllar, 2009). Detailed accounts by Spanish conquistadors and later the regional governments explain in great detail the quelling of indigenous uprisings, the capturing and enslavement of indigenous peoples and their forced labour in '*encomienda*' leading to an extensive depopulation of the region (Newson, 1995; Marín, 2002; Uzendoski, 2004). Introduced diseases likely played a role in the loss of the indigenous population, despite little recorded evidence of old World diseases appearing in the region (Newson, 1995). Contemporary and modern sources attributed the population decline primarily to high mortality rates (enforced labour, murder, starvation, infanticide) migration (forced and voluntary) and reduced fertility (Newson, 1995). Initial population estimates of the Quijos indigenous

people by the Spanish at contact was ca. 35,000, however, by ca. 1600 CE (around 50 years later) this had fallen to ca. 8600 individuals, indicating a 75 % decline in the population (Newson, 1995).

Palaeoecological analysis of the Huila sediments details a narrative of vegetation change mirrored by the change in the regional human population (Fig 5.2; page 88 and Appendix D; Figs. 8.6, 8.7, 8.8). The earliest sediments recording primarily pre-Hispanic indigenous occupation extends to ca. 1588. Palaeoecological proxies indicate an open cultivated landscape in which regular regional burning took place. While a pottery sherd recovered and dated to ca. 1423 provides direct evidence of people. This is followed by a period lasting from ca. 1588-1718, initiated by a brief spike in local burning during the period of indigenous uprisings against Spanish rule. Abandonment of the cultivated land is followed firstly by pioneer species and then the establishment of secondary forest. This is followed by the establishment of a structurally intact forest by ca. 1718, containing typical montane cloud forest taxa, such as Melastomataceae, Moraceae, *Hedyosmum*, *Weinmannia*, Fabaceae and Solanaceae. During the period of postcolonial Ecuadorian independence deforestation begins, from ca. 1822 decreasing forest cover and the introduction of cattle to the region opens up the landscape. This is gradual at first but by ca. 1950, increased erosion and cattle farming forms the mosaic landscape of secondary forest and pastures we see today. The montane forest of the Quijos Valley as described by Jameson (1858) and Orton (1875) was therefore not an ancient intact forests, but ca. 250 years of forest succession and recovery after the abandonment of the managed pre-Hispanic landscape.

In order to put the extent of human impact during the pre-Hispanic and European arrival periods into context, we can compare them to; 1) a pre-Human record (Chapter 4 Vinillos) which reveals the vegetation and landscape dynamics of the region prior to any human influence and to, 2) a modern pollen and fungal NPP record (Appendix D; Figs. 8.5, 8.6, 8.7) which represents the current mosaic landscape of cultivated fields and secondary forest. DCA was used to visualise the relationships within all of the terrestrial pollen and fungal NPP data (Fig 6.1 and 6.2). The pollen signal from mosaic landscape that we see today is most similar to that of the secondary forest than occurred after the initial indigenous uprising and during the depopulation of the region during the late 1500's and early 1600's. The pre-human arrival Vinillos assemblage, which represents a mature forest environment is most

similar to that of the montane forest that occurred during the period of quiescence in the region between ca. 1718-1822, when the indigenous population was at its lowest. The pollen data show that the signal from the pre-Hispanic period is clustered and different than during any other period of time from which samples were analysed (Fig. 6.1; group C).

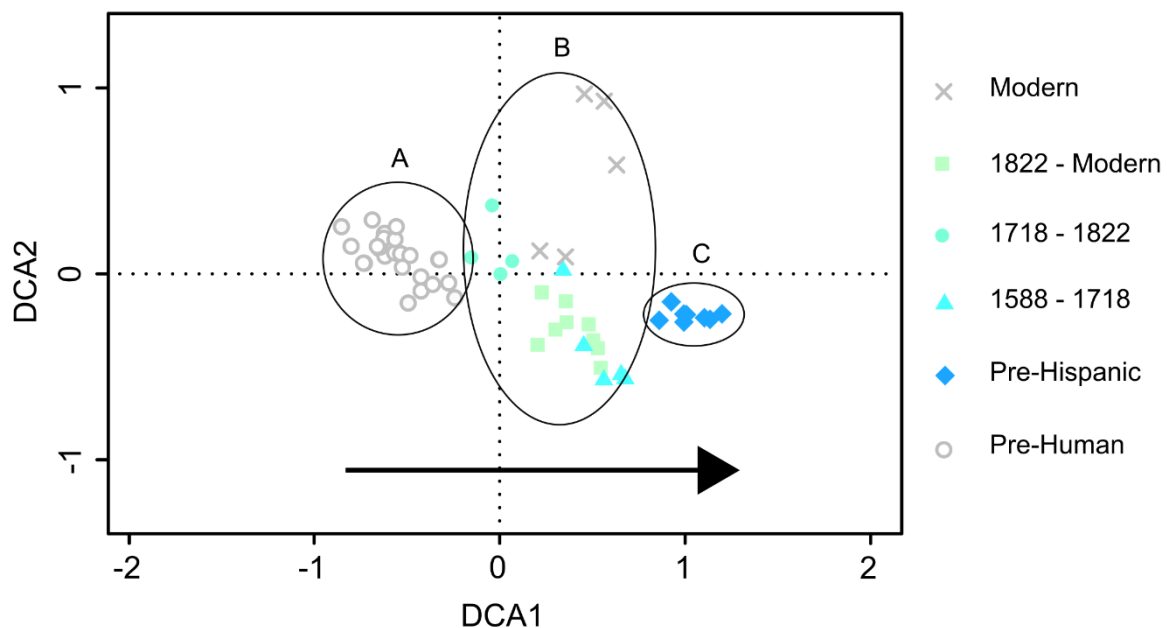


Figure 6.1 DCA of terrestrial pollen from all samples. Arrow represents increasing human impact. A) pre-human arrival (no human impact), B) indigenous depopulation and modern environment (variable human impact), C) pre-Hispanic (intensive human impact).

The horizontal axis of Fig. 6.1 (DCA1) is interpreted as representing pollen assemblages of increasing human impact, from a base of the pre-human glacial setting to most highly impacted pre-Hispanic landscape. This proposes that the pre-Hispanic landscape was characterised by vegetation representing more intensive human impact than we see in the landscape today. This is supported in the charcoal record (Fig. 5.2, page 88), where human initiated fires are most prevalent during the pre-Hispanic period and early European arrival, and contain the only evidence of cultivated plant species (*Zea mays*). This interpretation of a novel vegetation community in the pre-Hispanic landscape is upheld in the fungal NPP assemblage where all post-European contact samples are more similar to that of the pre-human arrival environment of Vinillos than that of the pre-Hispanic cultivated landscape (Fig. 6.2). The relationship between forest cover and fungal NPPs (Fig. 3.3; pages 47-48)

during the pre-Hispanic period form a statistically significant NPP assemblage with characterised by morphotypes *Neurospora*, IBB-16, HdV-201, OU-102 and OU-110, confined to < 8 % forest pollen taxa. This supports the hypothesis that the open, cultivated and fire prone landscape of the pre-Hispanic period was more impacted by human activity than during any of the other periods identified, from the pre-human arrival Pleistocene landscape to the modern mosaic landscape of secondary forest and cultivate fields and pastures we see today.

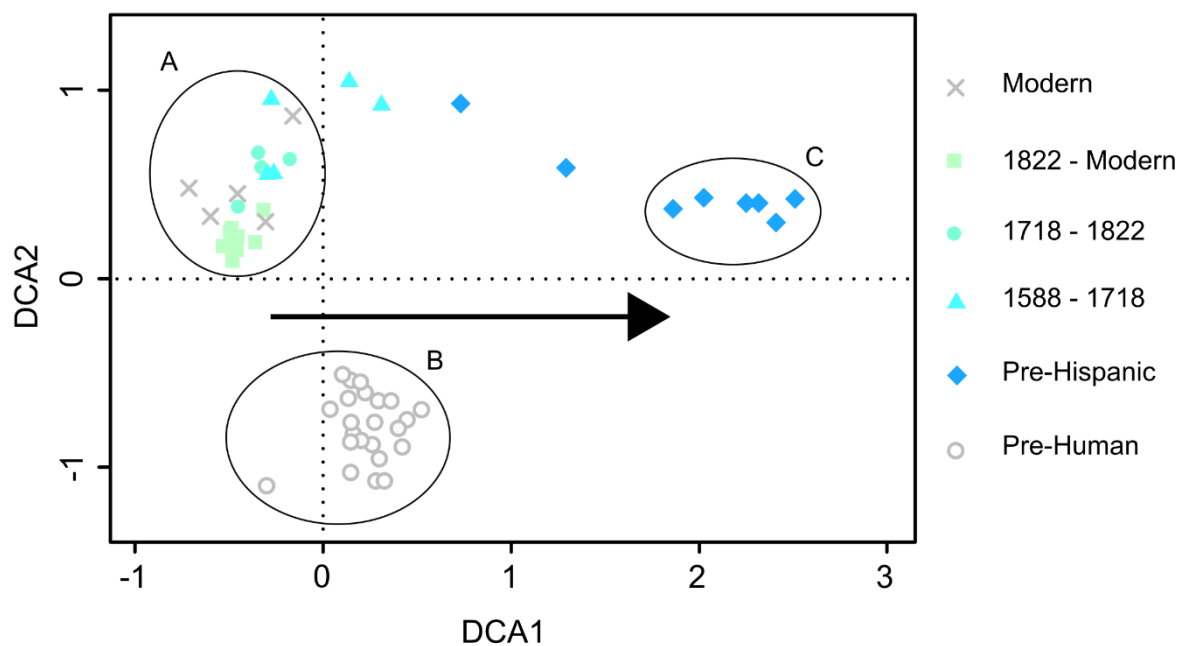


Figure 6.2 DCA of fungal NPPs from all samples. Arrow indicates increased disturbance by humans and volcanic activity. A) indigenous depopulation and modern environment (montane forest assemblage), B) pre-human arrival (glacial forest assemblage) and, C) pre-Hispanic (cultivated landscape assemblage).

6.4.2 Establishing an appropriate ecological baseline

Conservation and restoration of the mega-diverse montane forests of the eastern Andean flank is a priority in preventing the loss of biodiversity and maintaining essential ecosystem services (Myers et al., 2000; Josse et al., 2009; Anderson et al., 2011). Establishing ecological baselines for environments sensitive to human impact and climate change is therefore crucial in order to determine the scope of conservation and restoration required, and as a way of quantifying the effectiveness of ongoing strategies (Willis et al., 2010; Birks, 2012; Wood et al., 2017). Ecological data can demonstrate the short-term (< 100 years) response of ecosystems to change, while models can be used to predict future species distributions

under changing conditions (Elith & Leathwick, 2009). Palaeoecology allows us to observe empirically the interactions between ecosystems and environmental conditions over much longer time frames (1000's of years), and often to a resolution comparable to that of modern ecological studies. Over the last 20+ years numerous reviews have outlined the potential role that palaeoecology can play in incorporating a temporal dimension into conservation and restoration ecology (Birks, 1996, 2012, Willis et al., 2007a, 2007b, 2010; Davies & Bunting, 2010; Willis & Bhagwat, 2010; Vegas-Vilarrúbia et al., 2011; Nogué et al., 2017). However, few appear to have been actively incorporated into ongoing conservation strategies (Bush et al., 2014). This seeming lack of real-world progress underlies the intricacies of restoring an ecosystem to a hypothetical natural ecological baseline.

Identifying conditions prior to human driven vegetation change is a prerequisite of restoration if a natural ecological baseline is the desired state, so that restoration does not take place against a modified or shifted ecological baseline (*sensu* Pauly, 1995). In circumstances where managed or cultivated environments are to be maintained as determined by the ecosystem services they can provide (e.g. cultural landscapes), palaeoecology can still play a role in understanding ecosystem dynamics over the long-term. However, the application of hypothetical ecological baselines to a real world setting is problematic, even when multiple ecological baselines, from a number of points through time are available. The idea that ecological conditions can reach a steady state to which an ecosystem may be reverted to may not be possible, and the concept of a dynamic baseline incorporating predictions of environmental change and climate models may be required in order to inform long-term (10's to 100's years) conservation efforts.

Attempts at assessing natural baseline conditions within the Andes and Amazonia are limited, made difficult by the inaccessibility of tropical forests and the poorly constrained extent of past human activity. Attempting to establish a distinct natural ecological baseline for a region requires locating the first evidence of human impact, as well as establishing how the natural ecological baseline may have shifted through time in response to a changing climate and natural environmental processes. Humans first arrived in the Neotropics prior to the start of the Holocene (ca. 11.7 ka), immediately suggests that identifying a natural ecological baseline for the current climate period is unfeasible. An attempt to constrain a minimally human impacted baseline would require that the period of extensive human

impact which has occurred over the last ca. 5 ka be excluded, along with prolonged climate excursions such as the Mid Holocene Dry Event (MHDE) (Reich et al., 2012; Clement et al., 2015; Goldberg et al., 2016). However, the impact of human populations and climate across the Neotropics is variable. Lake Pata in the wettest part of the western Amazon exhibits a period of aridity 6-7 ka (Colinvaux et al., 1996; Bush, 2002; Bush et al., 2004a), at Lago Consuelo and Lake Titicaca in Peru it occurs around 9-5 ka and at 6 ka respectively (Baker et al., 2001; Bush et al., 2004b; Hanselman et al., 2011), while on the eastern Andean flank of Ecuador at Lake Surucucho little change is observed (Colinvaux et al., 1997). Valencia (2014) attempted to establish vegetation baselines for the high tropical Andes using a spacial distribution model for the distinctive high Andean taxon *Polylepis* which was then tested against a multiproxy palaeoecological reconstruction of lake sediments. When periods of time were excluded which exhibited divergent climate regimes (e.g. prior to the Holocene, during the MHDE) or potential human impact (post-MHDE) a period of around 10 ka was identified as a suitable natural ecological baseline. However, the practicalities of recovering long palaeoecological records from the volcanically active eastern Andean flank have been discussed, limiting the applicability of using a baseline that occurred ca. 10 ka to determine regional vegetation patterns. Therefore, identifying a more recent period unaffected by substantial climatic or human impact is necessary, which offers a greater prospect of finding multiple palaeoecological records. This is required all whilst maintaining a reasonable prospect of representing an ecological baseline that meets the ecosystem service requirements of an intact tropical montane cloud forest.

In this research vegetation and ecosystem processes were analysed prior to human arrival in South America (Chapter 4; Vinillos). This was then compared to samples covering approximately the last 700 years (Chapter 5; Huila) in order to determine if vegetation recovery during periods of low human population could be used as a potential, albeit shifted ecological baseline. The Huila record clearly shows vegetation recovery coeval to the historically recorded population decline in the Quijos Valley after European arrival. Fig. 5.2 (page 88) records the initial recovery of the montane forest environment through an increase in forest pollen taxa ca. 1588 CE which commences after a spike in macro-charcoal at the time of final indigenous uprisings against Spanish rule. Forest pollen taxa is seen to increase through the 17th century with a succession of pioneer and disturbance indicators,

initially Poaceae and *Cecropia*, followed by increasing proportions of typical montane forest taxa, such as Melastomataceae, Moraceae, *Hedyosmum*, *Weinmannia*, Fabaceae and Solanaceae. This initial recovery, analogous to a secondary forest environment is present between ca. 1588-1718 CE (Fig. 6.1), after which a transition to a more established montane forest environment occurs. This more established montane forest environment existing between ca. 1718-1822 CE and is represented by a pollen assemblage absent of disturbance indicators and dominated by pollen from the characteristic montane forest taxa. When plotted against all other pollen assemblages in a DCA, samples from this period fall out closest to that of a pre-human arrival pristine forests of the late-Pleistocene (Fig. 6.3). Therefore, this period of minimal human occupation, containing a structurally established montane forest with ecosystem functions and processes comparable to that of a pre-human impacted state, may represent our best most recent target from which to establish an appropriate ecological baseline. However, compositionally this forest community cannot represent an intact natural ecological baseline, due to its immaturity. Neotropical tree species often live for several centuries and as such the intensive disturbance that occurred during the pre-Hispanic period, less than 230 years prior to the beginning of the modern phase of deforestation would still have a profound impact on vegetation composition and diversity. Analysis of secondary forests growing in abandoned pastures in Puerto Rico indicate that after 30 to 40 years biomass, stem density and species richness are similar to that of mature forests, suggesting that rapid recover can occur in managed tropical landscape (Zimmerman et al., 2007). An aspect that may also favour montane forests to recover quicker than lowland forest communities is the resilience of Andean forests to regular perturbations (Stern, 1995; Crausbay & Martin, 2016). The active and dynamic landscape processes that perpetually disturb montane forests (e.g. volcanic eruptions, landslides) are a natural component of eastern Andean flank ecosystem dynamics and as such maybe analogous to past human impact.

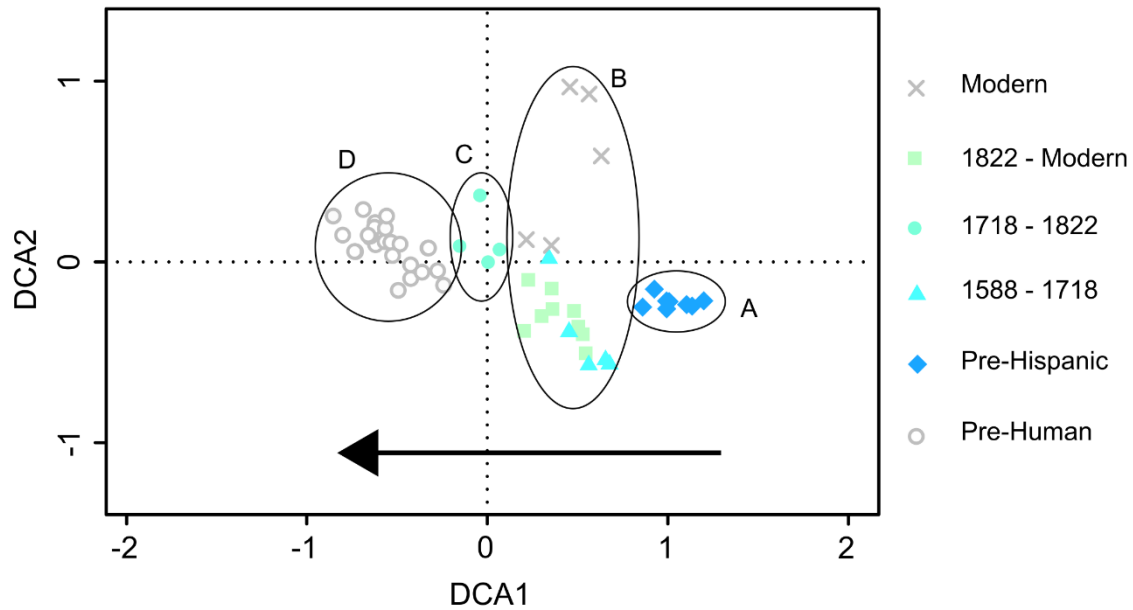


Figure 6.3 DCA of pollen taxa from all sample locations indicating succession from human impacted to pristine forest (arrow). A) open landscape, B) secondary/mosaic forest, C) mature forest, and D) pristine forest.

Attempting to establish natural ecological baselines near sites of long-term human habitation or archaeological sites are fraught with issues and should not be extrapolated out regionally, particularly in the heterogeneous landscape of the eastern Andean flank. The 49 cm's of lake sediment from Huila records approximately the last 700 years of human impact within the Quijos Valley. This record proves that short-cores taken from small lakes and bogs are useful in establishing local to extra-local, historical ecosystem dynamics and human impact in a biodiverse montane forest. As discussed above, the vegetation structure ca. 130 years after the start of forest recovery was composed of a vegetation community dominated by typical Andean taxa, potentially replicating the functional processes and providing many of the ecosystem services of a pristine montane forest. The vegetation exhibited no evidence of ongoing human impact (e.g. charcoal, pottery sherds, cultivars) or palynomorphs indicative of a disturbed forest environment (e.g. *Cecropia*, *Poaceae*, *Neurospora*). There are no substitutes for primary forest, although, studies often classify primary forest by the criteria of not being disturbed recently, and acknowledge that few forest today are likely to be pristine (Gibson et al., 2011). The baseline proposed in this study is unlikely to contain the biodiversity of an 'intact pristine forest'. However, the period of indigenous depopulation may represent the most practical ecological baseline to which

conservation strategies could aim. Ongoing environmental and climate change means that any restoration targets set now may become unsustainable in the future (Hobbs et al., 2009; Jackson & Hobbs, 2009). However, this baseline offers the opportunity to undertake restoration and conservation of pastures and forest fragments in partnership with rural and indigenous communities, while active management would allow for a resilient system to be established that can withstand the stresses of a changing climate and continuing human impact (Chazdon, 2008). This approach could be seen to establish a ‘cultural ecological baseline’, with the well-established understanding that it does not represent a pristine idealised landscape. This novel ecosystem would be one formed as a consequence of changes to species distribution, climate and land use (Hobbs et al., 2009). It is one representative of the modern landscape, containing many of the key ecosystem services required of a biodiverse tropical montane forest while retaining the important cultural elements of historic land use by the indigenous population.

6.5 Conclusions

The objective of this thesis was to characterise how the vegetation of the montane cloud forest of the eastern Andean flank of Ecuador has responded through time to changing human impact. Understanding how this biodiverse tropical forest has changed in the past is critical if we are to appreciate how current and future human impact will affect the ecosystem services that the montane forests provide, and how conservation and restoration of this globally important ecosystem should proceed. The key findings of the research undertaken include:

- *Low forest cover conditions are characterised by a distinctive fungal NPP assemblage.* Analysis of NPPs over a forest cover gradient indicate that periods of low forest cover within a montane setting form a distinctive assemblage characterised by types such as *Neurospora*, IBB-16, HdV-201, OU-102 and OU-110. However, NPPs appear to be a poor indicator of forest cover at higher levels.

- *Fire and low forest cover are the primary environmental drivers of NPP assemblages in a montane environment.*

Canonical correspondence analysis (CCA) of environmental gradients indicate the presence of fire is the strongest driver of NPP composition, characterised by types such as *Neurospora*, IBB-16, HdV-201, OU-102 and OU-110. This assemblage in conjunction with a low forest cover setting are suggestive of human deforestation and burning within montane cloud forests that do not burn naturally. Therefore, this NPP assemblage can be used as evidence of human disturbance in future palaeoecological studies in the montane cloud forest of the eastern Andean flank.

- *Volcanic activity was the primary non-climate driver of landscape-scale vegetation change prior to human arrival.*

Changes in palynomorph assemblage after periods of volcanic activity, indicated by tephra deposits, show that local vegetation population dynamics responded to these stochastic events. Despite these periodic deposits of ash on the montane forest, the regional vegetation community present on the eastern Andean flank during the last glacial period ca. 45-42 ka BP remained compositionally stable and able to recover from these local perturbations.

- *Pre-Hispanic land management locally impacted vegetation to a greater degree than modern practices.*

Intensive pre-Hispanic impact on the landscape formed novel pollen and NPP assemblages not observed since. These assemblages characterised an open environment with little forest cover that was regularly burned and cultivated. The distinctive combined assemblages formed by this activity may be used to aid identify further areas of pre-Hispanic land-use with the montane cloud forest of the eastern Andean flank.

- *Historically recorded depopulation of the indigenous people corresponds to a period of forest recovery in the Quijos Valley.*

Archaeological and historical evidence records the depopulation of the indigenous peoples of the Quijos Valley during the genocide that occurred after European arrival in the Americas. The palaeoecological proxies which provide evidence of pre-Hispanic landscape management in the Quijos Valley also record the change to a successional assemblage containing taxa typical of montane cloud forests. The depopulation of the region covaries with this change in vegetation ca. 1588 CE, suggesting a link between land abandonment and an increase in forest cover.

- *Forest succession took 130 years for a structurally mature montane cloud forest to be established.*

Following the pre-Hispanic period, and throughout the depopulation of the Quijos Valley secondary forest expanded to cover the previously managed landscape. Forest succession took at least 130 years to establish a vegetation assemblage containing little evidence of human disturbance and characterised by typical montane cloud forest taxa. This vegetation assemblage, although not directly comparable to a pristine forest, offers many of the ecosystem services provided by an intact montane cloud forest.

- *The period 1718-1822 CE may be used as a ‘cultural ecological baseline’ in the Quijos Valley.*

In the Quijos Valley the period following the succession of secondary forest to a more structurally intact montane cloud forest (ca. 1718-1822 CE) offers the potential to be used as a shifted ecological baseline. Natural ecological baselines are highly unlikely to be attainable within the montane cloud forest of the eastern Andean flank. Therefore, a ‘cultural ecological baseline’, reflecting the history of the region, from a period prior to recent deforestation offers a practical goal for future restoration and conservation priorities.

6.6 Recommendations for future work

This thesis establishes that pre-Hispanic indigenous peoples were a major driver of ecosystem dynamics in the montane cloud forest of the eastern Andean flank, and that

following depopulation of the region driven by European colonization forest expanded to cover the previously cultivated landscape of the Quijos Valley. This work has contributed to our understanding of how montane cloud forests have responded over the long-term to human impact, however, a variety of questions and avenues of research remain. These include:

- *Expand the range of palaeoecological proxies to refine the interpretation of the Quijos Valley.*

The Huila record contains a detailed account of vegetation change in response to changing human impact in the montane forest of the eastern Andean flank. Analysis of additional proxies such as diatoms, to determine lake conditions and nutrient input, phytoliths to increase identification of crops cultivated in the region and the use of aDNA as an independent proxy of local vegetation would improve our understanding of the impact humans have had on the montane cloud forest.

- *Extending the age of palaeoecological analysis in the Quijos region.*

The Huila record extends back around 700 years. Pushing the record of human impact back to the first arrival of people to the Quijos Valley would allow for a greater understanding of how the vegetation first responded to gradational increases in population. This also offers the prospect of establishing additional ecological baselines from periods of low intensity human impact and observing longer trends in vegetation succession.

- *Undertake a detailed review of the local ecosystem services provided by the montane cloud forest.*

The natural capital extracted from the montane forest of the eastern Andean flank provides a range of complex services to the people of Ecuador. Globally, tropical montane forests have been shown to deliver important goods and services to society in spite of a high rate of habitat destruction (Martínez et al., 2009; Higuera et al., 2013). However, a detailed review of the ecosystem services provided by the montane forest of the eastern Andean flank has yet to take place. Using the

categories established by the Millennium Ecosystem Assessment (2005), an overview of the supporting, provisioning, regulating and cultural services provided in the Quijos Valley is an essential first step toward restoration and conservation.

- *Improved understanding of modern pollen-vegetation relationships within montane cloud forests.*

Increasing the number of proxy training sets within the Andes and Amazon over environmental, geographical and human impacted gradients would allow for a more accurate interpretation of palaeoecological records.

- *Increase the number of palaeoecological records across the eastern Andean flank to account for regional variation.*

The eastern Andean flank is a dynamic and heterogeneous landscape and additional records are essential to account for regional variability in vegetation and human habitation. This step is essential if an accurate natural or cultural ecological baseline is to be used as a target for conservation and restoration.

'Ultimately, the future of a natural ecosystem depends not on protection from humans but on its relationship with the people who inhabit it or share the landscape with it.'

- William R. Jordan III, *in* The Sunflower Forest: Ecological Restoration and the New Communion with Nature, pp-16.

Chapter 7

7 References

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Chapter 8

8 Appendix

8.1 Appendix A – Ecological affinity of fungal NPPs

List of previously described NPP morphotypes found on the eastern Andean flank and information on their ecological affinity.

Amphirosellinia-type (formally within *Rosellinia*): Classified by Ju et al. (2004).

Amphirosellinia grow inside the bark of dicotyledonous trees (Ju et al., 2004; Gelorini et al., 2011).

Anthostomella fuegiana (HdV-4): Classified by van Geel et al. (1978). Ascospore occurs throughout a late Holocene peat bog in the Netherlands, attributed to Cyperaceae and Juncaceae host plants.

Cercophora-type 1 (HdV-112): Classified by van Geel et al. (1981, 1983) and van der Wiel (1982). *Cercophora* species are coprophilous or are associated with decaying wood, herbaceous stems and leaves (Lundqvist, 1972) and have been used as an indicator of animal dung at archaeological sites (van Geel et al., 1981, 1983, 2003; Buurman et al., 1995; van Geel & Aptroot, 2006). However, analysis by Cugny et al. (2010) was able to show no positive relationship between *Cercophora* and total grazing pressure and suggest presence is also linked to forested environments.

Cercophora-type 2 (HdV-1013): Classified by van Geel et al. (2011). Morphotype differs from HdV-112 based on variation in ascospore size and morphology. For ecology see *Cercophora*-type 1.

Conidiophores (HdV-96): Classified by van Geel (1976). Fungal remains of a heterogeneous group of dematiaceous genera (van Geel, 1976).

Coniochaeta cf. *ligniaria* (HdV-172): Classified by van Geel et al. (1983). *Coniochaeta* cf. *ligniaria* is a coprophilous or lignicolous fungus that has been found in Roman period soils

from meadows near populated settlement sites (van Geel et al., 2003) and have been linked to fluctuations during long term changes in humidity (van Geel et al., 2011).

Gaeumannomyces sp. or *Clasteropsprion caricinum* (HdV-126): Classified by Pals et al. (1980). Hyphopodia of leaf parasites associated with Cyperaceae (Deacon, 1976; Walker, 1980; van Geel & Aptroot, 2006).

Glomus sp. (HdV-207): Classified by van Geel et al. (1989). *Glomus* is an arbuscular mycorrhizal fungus which occurs on a wide range of vascular plant. Increased presence of *Glomus* in lake sediments has been linked to soil instability and increased erosional processes (Anderson et al., 1984).

HdV-16A: Classified by van Geel et al. (1981). van Geel et al. (1981) indicate that Type HdV-16A occurs in mesotrophic conditions in peat during dry phases and decreases or is absent during moist oligotrophic phases.

HdV-123: Classified by Pals et al. (1980). Occurs commonly in bog or marsh type environments in the Netherlands associated with *Betula* and is considered to be an indicator of eutrophic to mesotrophic conditions (Pals et al., 1980; van Geel et al., 1981; Bakker & van Smeerdijk, 1982).

HdV-201: Classified by van Geel et al. (1989). Morphotype was recorded within drier microhabitats on standing culms of helophytes or on plant remains in temporary desiccated pools (van Geel et al., 1989).

HdV-495: Classified by van Smeerdijk (1989). A fungi associated with the epidermal remains of Poaceae in open and semi-open landscapes in Europe (van Smeerdijk, 1989; Cugny et al., 2010) and from the cloud forest and Páramo of the Venezuelan Andes (Montoya et al., 2010).

HdV-733: Classified by Bakker and Smeerdijk (1982). Morphotype was recorded from a mesotrophic helophyte marsh dominated by *Phragmites* sp.

HdV-1058: Classified by van Geel et al. (2011). Morphotype present throughout much of the late Pleistocene and Holocene of equatorial tropical east Africa, the highest concentration occurring during the climatically wet early Holocene.

IBB-16: Classified by Montoya et al. (2010). Ascospores found in modern samples from the Páramo of the Venezuelan Andes (Montoya et al., 2010).

IBB-25: Classified by Montoya et al. (2010). IBB-25 is found in surface samples from the cloud forest and Páramo of the Venezuelan and Colombian Andes (Hooghiemstra, 1984; Montoya et al., 2010).

IBB-259: Classified by López-Vila et al. (2014). Morphotype occurs in low abundance within a human disturbed montane/subalpine region of the Spanish Pyrenees.

IBB-262: Classified by López-Vila et al. (2014). Morphotype was identified in low abundance within a montane/subalpine fir forest (*Abies* sp.) of the Spanish Pyrenees.

Kretzschmaria (formerly *Ustulina*) *deusta* (HdV-44): Classified by van Geel (1978). A parasitic fungus of deciduous trees causing soft wood rot of stumps and dead roots (van Geel & Andersen, 1988; van Geel & Aptroot, 2006). Occurs on a variety of host trees in Europe and North America including taxa which occur within Andean montane forests, such as *Alnus* sp. and *Ilex* sp. (van Geel, 1978; van Geel & Andersen, 1988).

Neurospora spp. (syn. *Gelasinospora* spp. see García et al. (2004)) (HdV-1093 / HdV-1351): *Neurospora* spp. is suggested to be a carbonicolous, lignicolous or coprophilous fungi (Lundqvist, 1972; van Geel, 1978) with a life cycle adapted to respond to fire (Jacobson et al., 2006).

Podospora-type (HdV-368): Classified by van Geel et al. (1981). *Podospora*-type represents coprophilous fungi often found in relation to human activity and/or herbivorous fauna (van Geel et al., 1981, 2003, 2008; Almeida-Lenero et al., 2005).

Rosellinia-type (UG-1174): Classified by Gelorini et al. (2011). *Rosellinia*-type is widespread throughout temperate and tropical regions and commonly found on decaying herbaceous stems and deciduous woods of dicotyledonous plants (Petrini, 2003; Gelorini et al., 2011).

Savoryella curvispora-type. Classified by Bakker and van Smeerdijk (1982). Morphotype is analogous to HdV-715 (Bakker & van Smeerdijk, 1982) from Europe and UG-1120 (Gelorini et al., 2011) from East Africa. Bakker and van Smeerdijk (1982) suggest a preference for eutrophic to mesotrophic helophyte marsh condition, while Ho et al. (1997) reported its presence on submerged wood in South-East Asia and South Africa.

Sporormiella-type (HdV-113): Classified by Ahmed and Cain (1972) and van Geel et al. (2003). *Sporormiella* are coprophilous fungi that are associated with herbivores (Davis, 1987; Comandini & Rinaldi, 2004) and have been used as a proxy to determine herbivore populations and extinctions (Burney et al., 2003; Gill et al., 2009; Raper & Bush, 2009; Baker et al., 2013).

Sordaria-type (HdV-55): Classified by van Geel (1976) and van Geel et al. (1981). *Sordaria* species are predominantly coprophilous (Lundqvist, 1972; Richardson, 2001; van Geel & Aptroot, 2006) but may include non-coprophilous species which occur in soil and on seeds (Guarro & von Arx, 1987).

Sordariales: Includes several morphotypes within this order but without genus identification (Lundqvist, 1972; Bell, 2005).

TM-211: Classified by Cugny et al. (2010). Morphotype identified as *Coniochaeta* B, from modern surface samples from a range of vegetation habitats within the French Pyrenees.

UG-1194: Classified by Gelorini et al. (2011). Morphotype present from lake sediment surface samples from western Uganda.

Xylariaceae-type: Morphotype may contain several species based on size variation belonging to the family Xylariaceae (Whalley, 1993; Petrini, 2003). Xylariaceae are cosmopolitan and occur as saprotrophic and coprophilous fungi and as endophytes on a variety of host plants (Whalley, 1993).

8.2 Appendix B – Newly identified fungal NPP morphotypes

Descriptions on new fungal morphotypes assigned with the prefix “OU-” (The Open University). Note: Three NPP morphotypes described here were not included elsewhere in the thesis for two reasons: (i) OU-103 and OU-117 do not feature in any palynomorph graph as they occurred below the 2 % cut-off, and (ii) OU-114 is excluded from statistical analysis as it only occurred in a single sample. All descriptions and measurements are based on a minimum of five individuals.

OU-5 (Fig. 8.1, 1) – Ascospores, fusiform, 1-septate, slightly constricted at septum (20.3 – 23.1 μm x 5.9 – 6.8). Cells joined through the septa and roughly equal in size.

OU-18 (Fig. 8.1, 2) – Ascospores, fusiform, 1-septate, slightly constricted at septum (29.3 – 34.9 μm x 9.4 – 9.8 μm). Cells symmetrical, gently curving, light brown in colour, ends taper to a rounded point which is often crumpled.

OU-28 (Fig. 8.1, 3) – Fungal spores, narrowly fusiform, slightly curved, unequal and asymmetrical. Cell walls smooth, peach to light brown in colour. Three, five or seven septate, middle septum slightly constricted, distal cells tapering to a rounded end, walls at tips thinning. Subtypes have been defined for this morphotype according to the number of cells/septa as it follows: Form-A (4 cells; 75.0 – 85.1 μm x 8.0 – 10.5 μm), Form-B (6 cells; 79.9 – 97.1 μm x 8.8 – 9.6 μm), Form-C (8 cells; 93.4 – 103.8 μm x 9.3 – 11.4 μm).

OU-35 (Fig. 8.1, 4) – Ascospores, fusiform, 1-septate, strongly constricted at septum (20.7 – 24.8 μm x 9.4 – 11.8 μm). Cells brown, taper towards each aperture, apertures 1.1 – 1.9 μm wide.

OU-100 (Fig. 8.1, 5) – Ascospores, fusiform, 3-septate, slightly constricted at middle septum. Cells asymmetric, smooth walled (31.4 – 42.3 μm x 11.8 – 13.1 μm). Central cells brown (13.4 – 10.1 μm), distal cells tapered, light brown to occasionally subhyaline (8.0 – 5.3 μm).

OU-101 (Fig. 8.1, 6) – Fungal spores, 5 to 6-septate, slightly constricted at septa. Cells asymmetric, smooth walled (24.7 – 30.6 μm x 7.7 – 10.3 μm). Central cells brown becoming light brown to subhyaline at terminal cells. Proximal cell rounded with truncated end, distal cell hemispherical with apical pore (1.8 – 2.1 μm).

OU-102 (Fig. 8.1, 7) – Fungal spores, conidia, 3-septate ($19.2 - 22.1 \mu\text{m} \times 12.7 - 15.0 \mu\text{m}$ excluding proximal cell). Cells are dark brown and asymmetrical, distal cell subhyaline and tapered with an apical pore. Proximal cell hyaline and often absent ($3.1 - 4.9 \mu\text{m}$).

OU-103 (Fig. 8.1, 8) – Fungal spores, slightly ellipsoid, 2-septate ($30.6 - 40.6 \mu\text{m} \times 10.6 - 14.8 \mu\text{m}$). Cells dark brown, asymmetrical. Distal cell has aperture ($< 1 \mu\text{m}$).

OU-104 (Fig. 8.1, 9) – Fungal spores, conidia, 3-septate, slightly constricted at septum ($26.2 - 32.1 \mu\text{m} \times 12.4 - 14.7 \mu\text{m}$). Distal cell brown, hemispherical, cells decreasing in size towards proximal cell. Proximal cell light brown, rounded, with apical pore. OU-104 is tentatively assigned to *Trichocladium* sp., which are often observed on submerged wood in fresh water environments (Goh & Hyde, 1999).

OU-105 (Fig. 8.1, 10) – Fungal spores, conidia, 2-septate ($19.4 - 24.6 \mu\text{m} \times 10.9 - 12.4 \mu\text{m}$). Distal cell dark brown, hemispherical. Proximal cell rounded, light brown. This type is tentatively assigned to *Endophragmiella* sp.

OU-106 (Fig. 8.1, 11) – Fungal spores, conidia, 2-septate ($15.1 - 17.7 \mu\text{m} \times 6.8 - 8.0 \mu\text{m}$). Distal cell brown, hemispherical. Proximal cell subhyaline, rounded, with apical pore.

OU-107 (Fig. 8.1, 12) – Ascospores, fusiform, 1-septate, slightly constricted at the septum ($34.1 - 39.9 \mu\text{m} \times 8.7 - 10.6 \mu\text{m}$). Dark brown, slightly curved, variable number of parallel longitudinal distal furrows.

OU-108 (Fig. 8.1, 13) – Ascospores, fusiform, 1-septate ($37.4 - 44.0 \mu\text{m} \times 11.9 - 16.1 \mu\text{m}$). Cells often asymmetrical. Cells taper to rounded point, with small ($< 1 \mu\text{m}$) inset apical pore.

OU-109 (Fig. 8.1, 14) – Fungal spores, elliptical, 1-septate ($24.6 - 29.9 \mu\text{m} \times 11.8 - 12.4 \mu\text{m}$). Cells often asymmetrical.

OU-110 (Fig. 8.1, 15) – Ascospores, 4 individual brown curved fusiform cells ($23.8 - 26.1 \mu\text{m} \times 16.8 - 18.5 \mu\text{m}$). Individual cells $5.5 - 6.0 \mu\text{m}$ wide.

OU-111 (Fig. 8.1, 16) – Ascospores, elliptical, single celled ($21.5 - 28.2 \mu\text{m} \times 19.1 - 22.3 \mu\text{m} \times 16.7 - 20.0 \mu\text{m}$). Spores bilaterally flattened, dark brown, single protruding apical pore. Flattened sides dark brown (i), light brown band around spore (ii).

OU-112 (Fig. 8.1, 17) – Fungal spores, fusiform to elliptical, often asymmetrical (31.2 – 37.1 μm x 15.8 – 19.3 μm). Spore dark brown, protruding apertures at either end (1.0 – 1.8 μm).

OU-113 (Fig. 8.1, 18) – Fungal spores, curved fusiform, single celled (45.0 – 50.1 μm x 7.0 – 7.6 μm). Germ split on inner curve (14.6 – 15.8 μm long).

OU-114 (Fig. 8.1, 19) – Ascospores, elliptical, single cell (22.8 – 28.8 μm x 11.4 – 17.7 μm). Spores light brown, with single apical pore, cell walls thicken around middle. Found in single sample in Lake Huila record. Tentatively assigned to the Sordariales.

OU-115 (Fig. 8.1, 20) – Fungal spores, elliptical, single celled (24.5 – 28.4 μm x 16.9 – 21.6 μm). Brown with equatorial dark band, single pore offset from apex, cell wall thickens around pore (2.2 – 3.0 μm).

OU-116 (Fig. 8.1, 21) – Fungal spores, flask shaped with flat base (triangular-shaped with rounded vertices), single celled (19.2 – 23.0 μm x 15.4 – 21.5 μm). Dark brown, single pore at apex (1.3 – 1.8 μm).

OU-117 (Fig. 8.1, 22) – Fungal spores, ellipsoidal, single celled (27.7 – 32.0 μm x 17.5 – 24.3 μm). Cell covered in small circular craters (1.7 x 2.9 μm in diameter and 1.1 x 2.4 μm apart). Single pore at apex with thickened wall.

OU-118 (Fig. 8.1, 23) – Ascospores, narrowly fusiform to elliptical, single cell (22.9 – 29.4 μm x 8.8 – 10.5 μm). Spore light brown, 4 parallel longitudinal furrows, slightly protruding apertures at either end.

OU-119 (Fig. 8.1, 24) – Fungal spores, inequilateral, single cell (19.4 – 25.1 μm x 10.9 – 11.5 μm). Cell, dark brown with one side straight. One end truncated (2.8 – 3.9 μm), other tapering to an angled protruding hyaline apex.

OU-120 (Fig. 8.1, 25) – Spherical fungal spores, smoothed, thick walled, dark brown (14.4 – 15.8 μm). Single pore (2.1 – 2.8 μm).

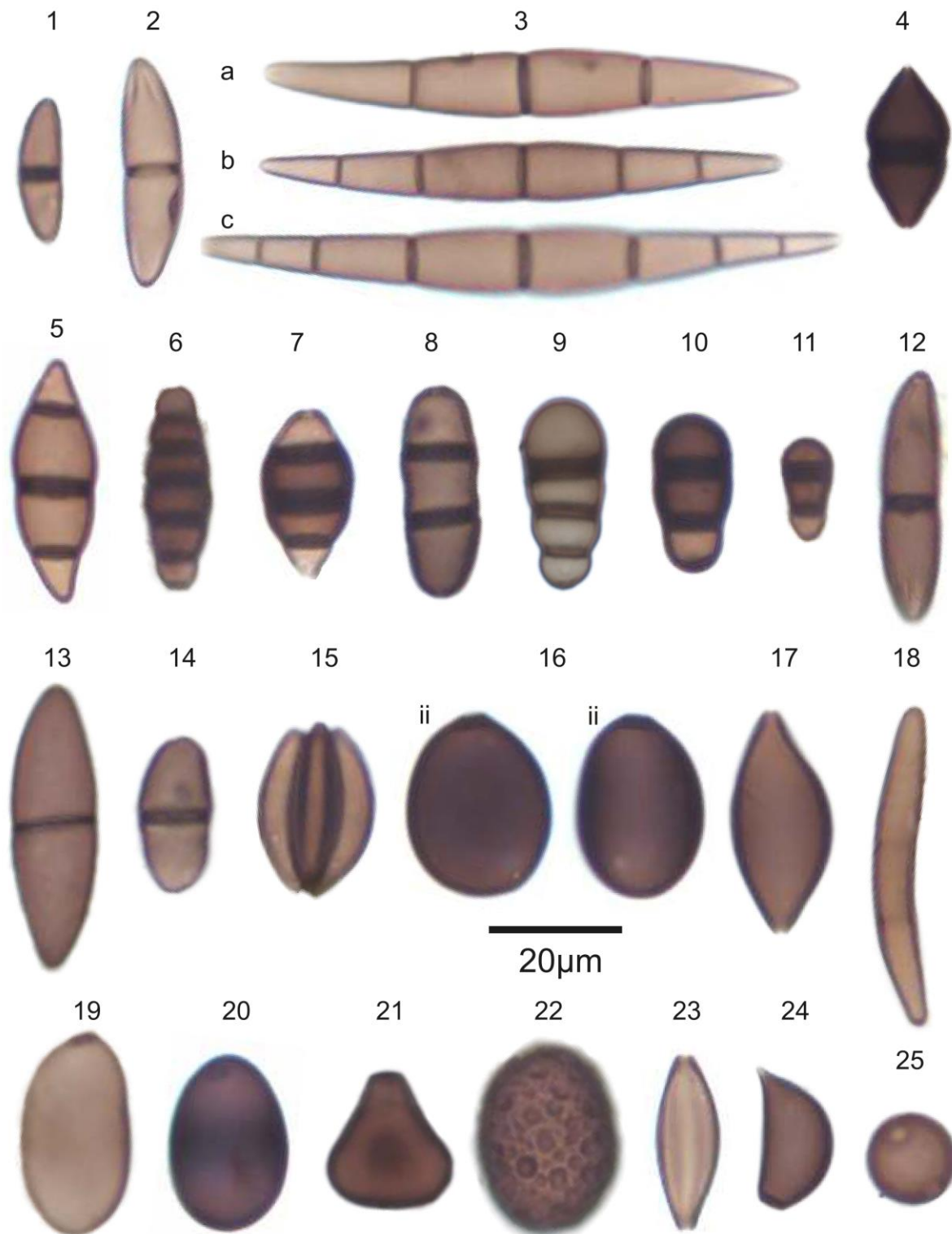


Figure 8.1 New fungal morphotypes described from the eastern Andean flank of Ecuador. Conidia positioned with proximal cell at bottom. 1, OU-5; 2, OU-18; 3, OU-28 a-c; 4, OU-35; 5, OU-100; 6, OU-101; 7, OU-102; 8, OU-103; 9, OU-104; 10, OU-105; 11, OU-106; 12, OU-107; 13, OU-108; 14, OU-109; 15, OU-110; 16, OU-111; 17, OU-112; 18, OU-113; 19, OU-114; 20, OU-115; 21, OU-116; 22, OU-117; 23, OU-118; 24, OU-119; 25, OU-120.

8.3 Appendix C – Chapter 5 additional figures

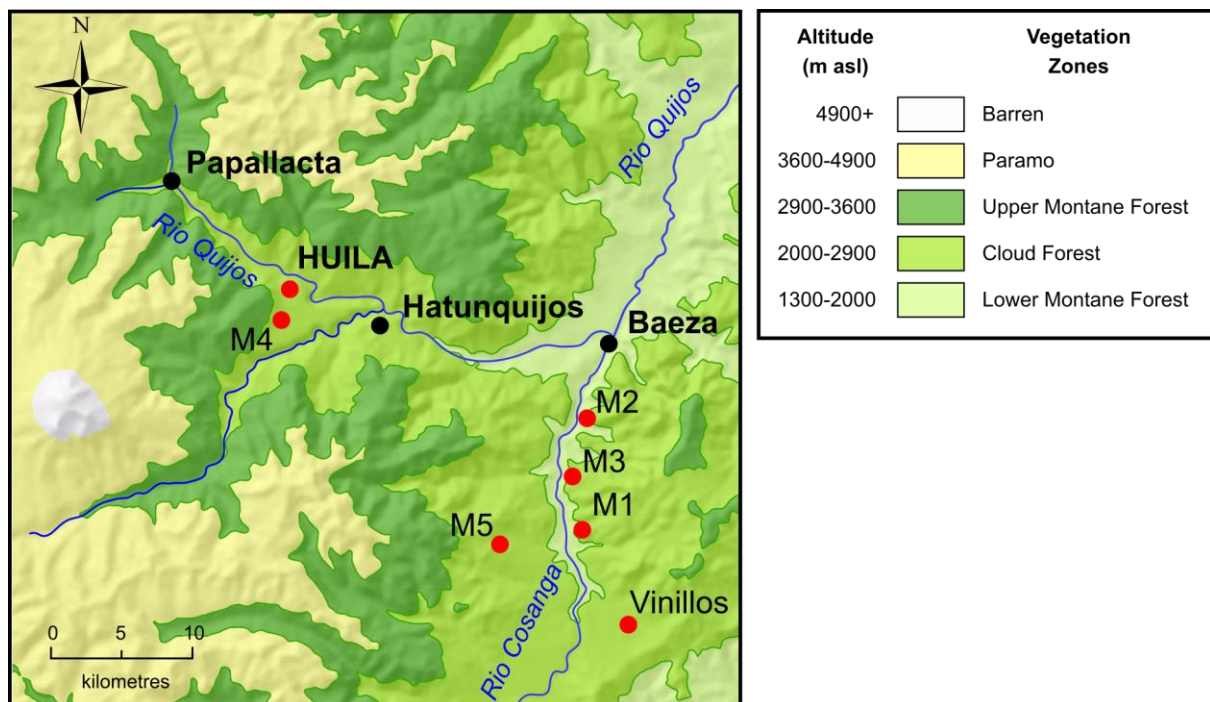


Figure 8.2 The Quijos Valley. Vegetation zones are based on those of Sierra (1999). Black circles indicate population centres. The indigenous village of Hatunquijos no longer exists, the position is recorded in Newson (1995). Red circles indicate the location of the sedimentary records (Huila and Vinillos) and modern surface samples (M1-M5).

Table 8.1 Details and locations of samples taken.

Study site	Age	Location	Substrate	No. of samples	Altitude (m asl)	Modern vegetation
Lake Huila	1ka-recent	S 00° 25.405, W 78° 01.075	Lake sediment	26	2608	Pasture
Vinillos	45ka-42ka	S 00° 36.047, W 77° 50.814	Sediment	26	2090	Secondary
M1	Modern	S 00° 32.930, W 77° 52.655	Moss polster	1	1925	Secondary
M2	Modern	S 00° 30.260, W 77° 52.598	Moss polster	1	1801	Riparian
M3	Modern	S 00° 32.278, W 77° 52.624	Wet soil	1	1798	Riparian
M4	Modern	S 00° 26.608, W 78° 00.431	Wet soil	1	2611	Secondary
M5 (Erazo)	Modern	S 00° 34.127, W 77° 53.970	Lake surface sediment	1	2306	Secondary

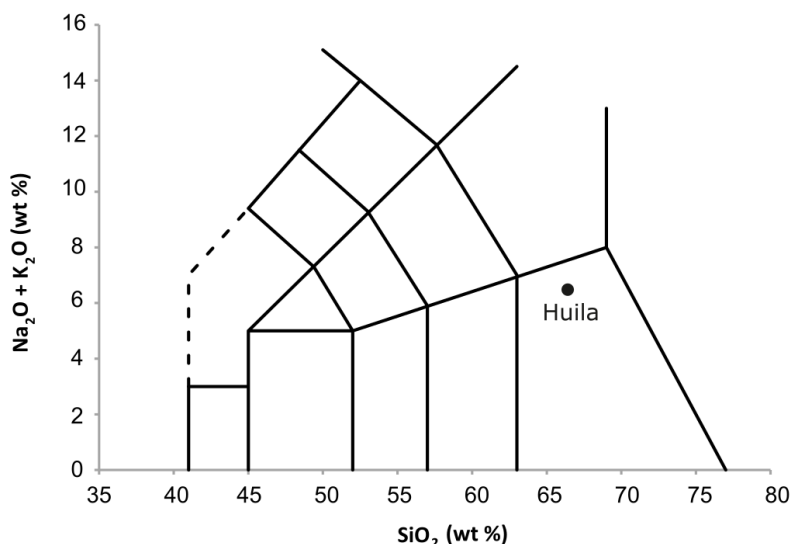


Figure 8.3 TAS diagram. Geochemical data from X-Ray florescence (XRF) analysis plotted onto a total alkali-verses-silica (TAS) diagram characterises the Lake Huila volcanic tephra layer as a dacite.

Table 8.2 Geochemistry of standards and the Huila tephra layer using XRF. *Loss on ignition (LOI) was undertaken at 550°C for 2 hours.

wt. %	WS-E	WS-E	WS-E	OU-3	OU-3	OU-3	HUILA
order	3	5	Recommend	1	4	Recommend	2
SiO ₂	51.06	51.11	51.10	73.99	73.97	74.09	66.17
TiO ₂	2.438	2.426	2.425	0.219	0.221	0.224	0.375
Al ₂ O ₃	13.95	13.98	13.78	11.05	11.06	11.11	16.28
Fe ₂ O ₃ (T)	13.20	13.18	13.15	3.86	3.84	3.83	2.62
MnO	0.174	0.170	0.171	0.091	0.091	0.090	0.056
MgO	5.62	5.62	5.55	0.05	0.04	-	1.95
CaO	9.05	9.07	8.95	0.21	0.21	0.20	3.56
Na ₂ O	2.43	2.43	2.47	3.69	3.72	3.68	4.53
K ₂ O	1.00	0.99	1.00	4.53	4.53	4.55	1.94
P ₂ O ₅	0.306	0.308	0.302	0.019	0.016	-	0.157
LOI*	0.85	0.85	0.85	1.82	1.82	1.82	2.38
Total	100.09	100.13	99.75	99.52	99.52	99.59	100.00

Table 8.3 Modern population within the region identified as the Quijos Chiefdom / Gobernación de Los Quijos. *Information from Ecuadorian census <http://www.ecuadorencifras.gob.ec/censo-de-poblacion-y-vivienda/>

Province	Canton	Population (2001)*	Population (2010)*	Area (km ²)
Napó	Archidona	18,551	24,969	3,029
	El Chaco	6,133	7,960	3,473
	Quijos	5,505	6,224	1,577
Orellana	Loreto	13,462	21,163	2,127
TOTAL		43,651	60,316	10,206

8.4 Appendix D – Detailed palynomorph and charcoal diagrams

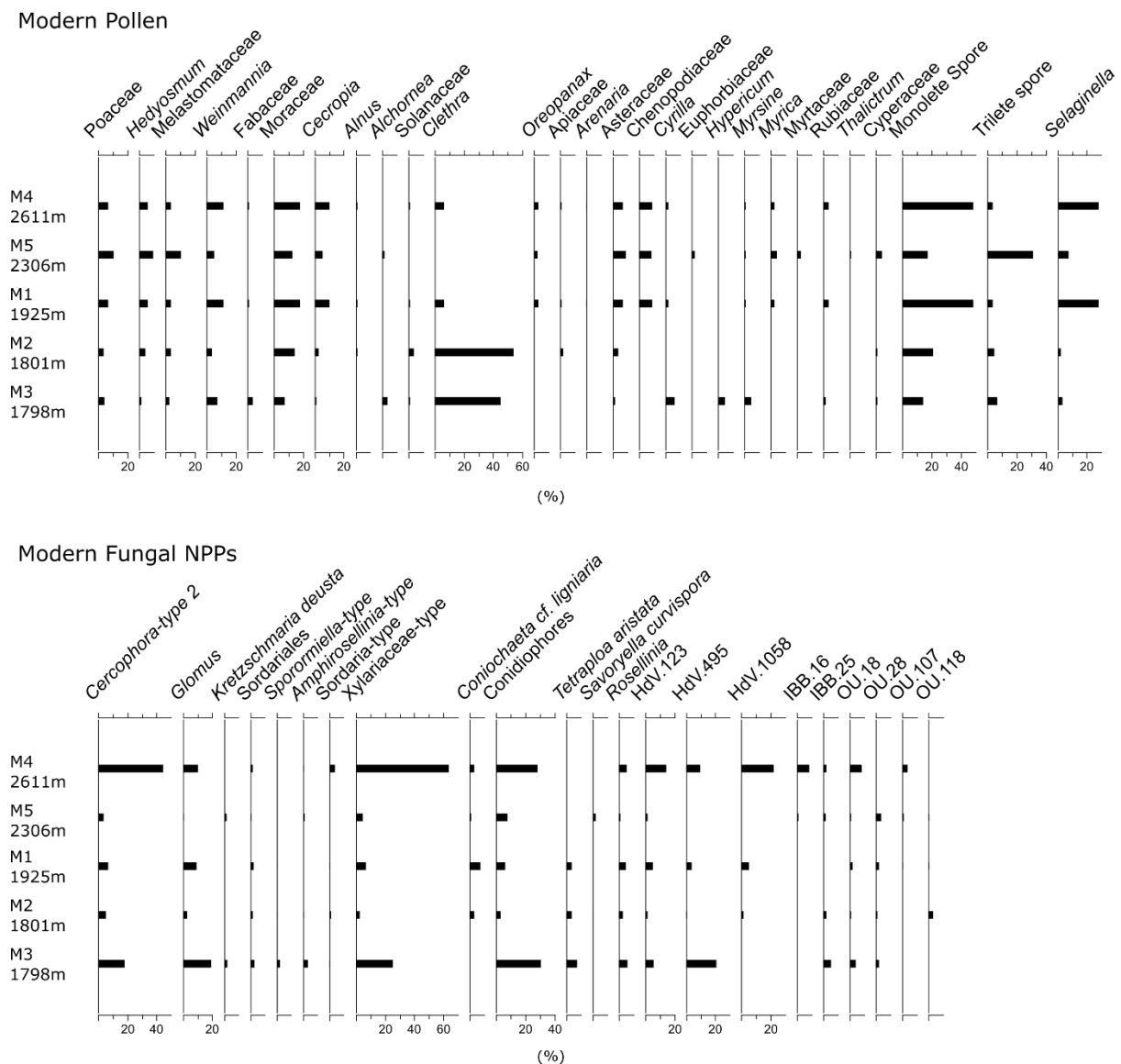
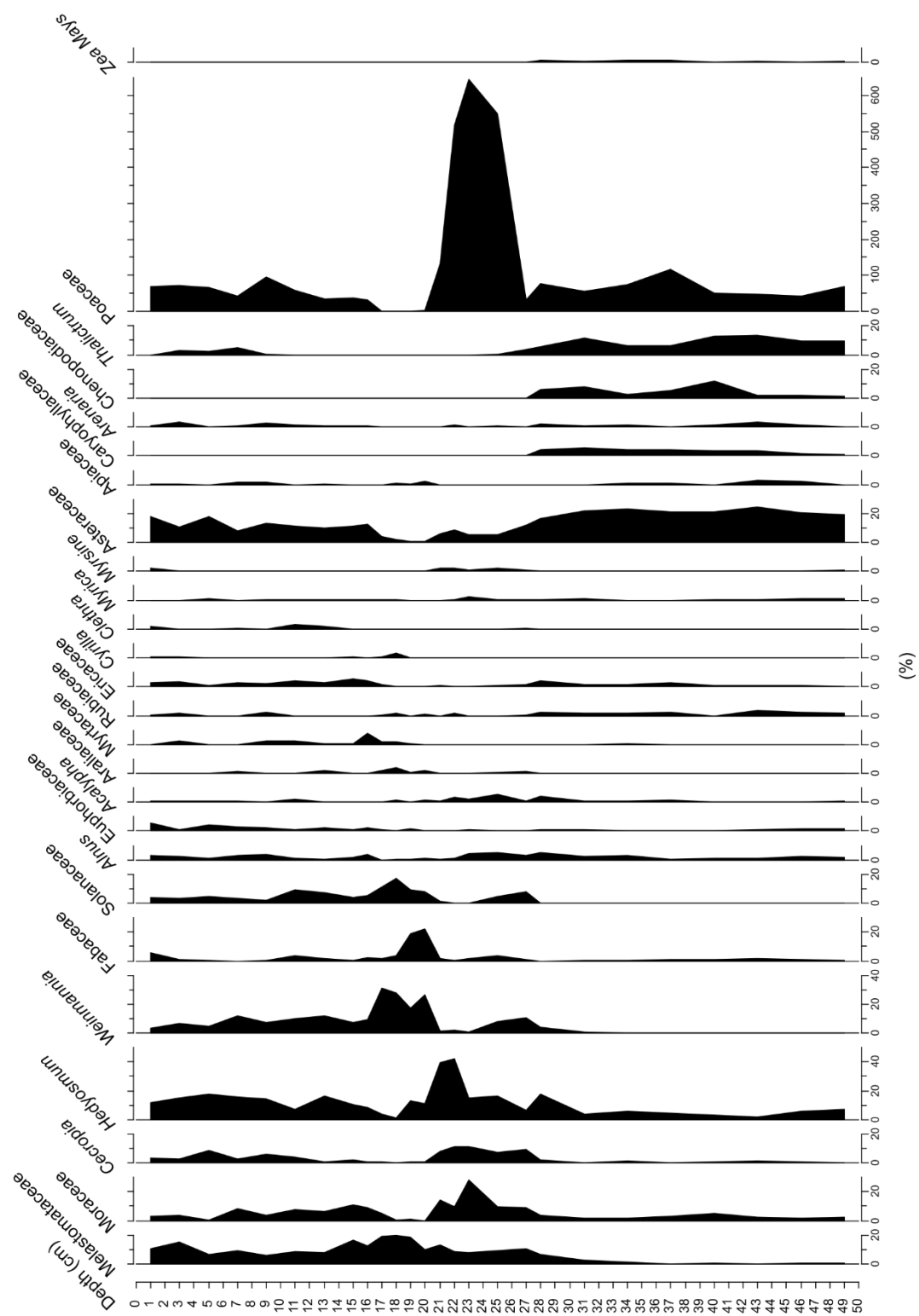


Figure 8.4 Modern pollen and fungal NPP diagrams. Samples plotted on an increasing altitudinal gradient.



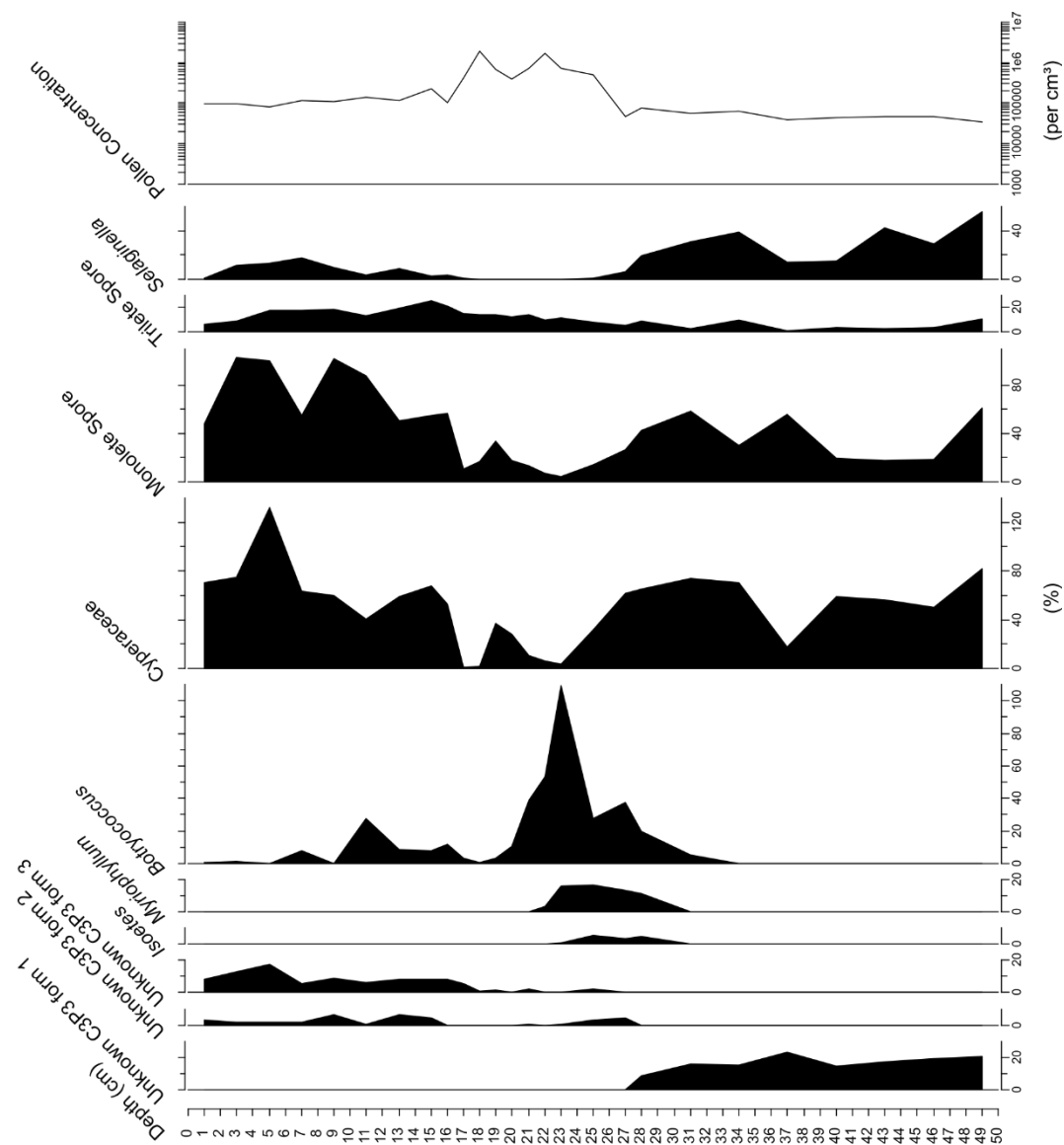
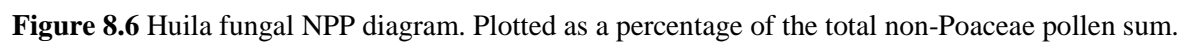


Figure 8.5 (Page 164-165) Huila pollen diagram. Pollen count incorporates terrestrial taxa excluding Poaceae. Pollen percentage diagram of taxa that occur at > 2% and *Zea mays*.



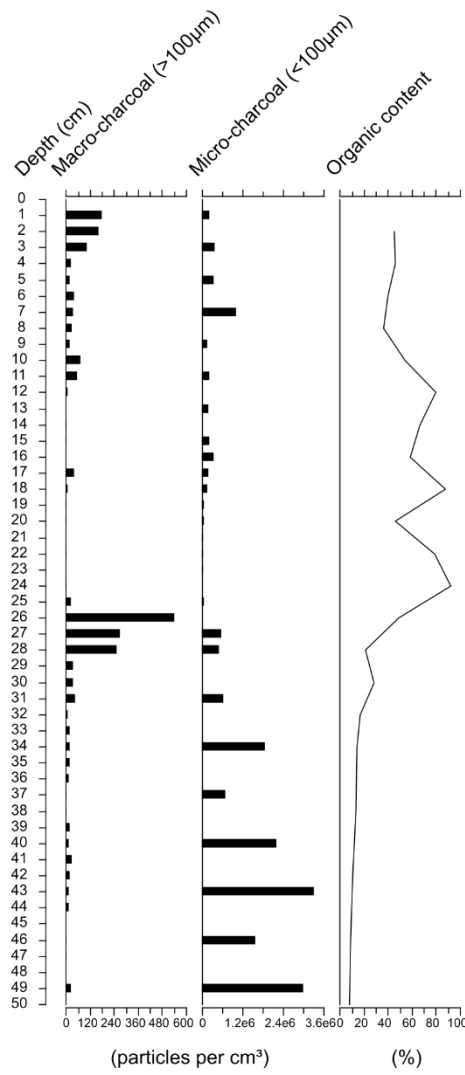


Figure 8.7 Macro- Micro-charcoal and organic content diagram of Huila.

8.5 Appendix E – Data storage

Raw data is contained on the attached CD. Palynological and charcoal data will also be entered onto Neotoma <https://www.neotomadb.org/> and the Global Charcoal Database <http://www.paleofire.org/index2.php> following the publication of the relevant manuscripts.